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RULES AND MECHANISM OF INHIBITION AND CORRELATION IN THE REGENERATION OF *BRYOPHYLLUM CALYCINUM*

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(WITH FORTY-ONE FIGURES)

I. Introduction

In the phenomena of regeneration the problem of correlation appears, that is, the influence of the whole on the part. A part cut out from a whole organism may regenerate, while no such regeneration will occur so long as the part is not separated from the whole. What are the forces inherent in the whole which exercise the control over the part resulting in the prevention of regeneration?

We cannot form a definite idea of this inhibitory mechanism until we know the laws or rules underlying this prevention of regeneration or growth in the normal plant. Only if we succeed in finding such rules and if they are sufficiently simple can we with any hope of success begin to draw conclusions concerning the nature of the mechanism underlying these phenomena of inhibition and correlation. The reason why it is difficult to find such laws lies in the fact that the phenomena of regeneration in most organisms are too complicated or too indeterminate for such a purpose, and we are compelled to look for an organism which is especially favorable for such a purpose. The tropical plant *Bryophyllum calycinum* is apparently such an organism, and the writer has succeeded in finding some rules governing the phenomena of inhibition and

correlation of growth. These rules are so simple and transparent that they form, in the opinion of the writer, a securer basis for hypothesis than is offered by most former experiments in this direction which have not led to such simple rules.

The advantage of this plant for the study of the problem of regeneration lies in the fact that shoots can grow out only from definitely located buds in the stem and in the notches of the leaf. The "Anlagen" of roots are not so definitely located, and roots may grow out apparently from practically any spot on the stem of the plant; they are, therefore, not so appropriate for the establishment of definite and simple rules of inhibition, and their growth will not be considered in this paper.

One bud is located in each notch of a leaf of *Bryophyllum calycinum;* when such a notch begins to grow it forms first roots and later shoots. It is well known that if the leaves of this plant are cut off and put on moist soil (or suspended in moist air) they will form roots and shoots from their notches. This is the mode of propagation of this plant. The question is: Why does a leaf not form roots and shoots in its notches so long as it is in connection with a healthy plant? The buds in the notches of the leaf are not the only ones which are inhibited from growing when forming parts of the whole; the buds on the stem, one of which is found in the axilla of each of the two leaves in each node, are in the same condition, and the same question may be raised, namely: Why do not these buds grow out as long as they form part of a plant, while if isolated they may grow into shoots?

A very few words will suffice to show that the stimulus of the wound is not responsible for the growing out of buds, though the conditions at the edge of the wound are responsible for the healing or covering of the wound by the spreading of epithelial cells over the area laid free by the wound; and they may possibly be directly responsible for the callus formation in the case of plants. When we break off a leaf of *Bryophyllum*, the notches of the leaf will grow out into roots and shoots, but these notches are far away from the cut end of the stalk of the leaf. Moreover, as a rule, the notches in the middle of the leaf will grow out first, and not those nearest the wound caused by the cutting or breaking off of the leaf. It is

plainly impossible, therefore, to connect in any way the growth of the notches of a leaf with the "stimulus" of the wound. The same may be said for the growth of roots in the main stem of the plant, which may take place several inches away from the seat of injury. We need not dwell on this point any further, since this is generally conceded. It is chiefly in animals that we find regeneration localized at the wound; but this is apparently due to the fact that in such animals any cells may give rise to new growth, while in *Bryophyllum calycinum* the power of giving rise to shoots is restricted to buds located in definite places in the plant.

II. Isolation as the cause of regeneration

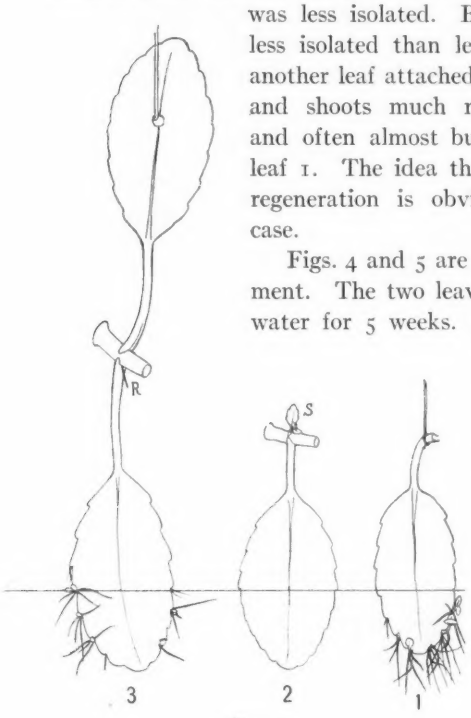
It is generally stated that "isolation" is responsible for regeneration, inasmuch as isolation would release the leaf from the inhibiting influence which the whole has on each part.[1] It is obvious, however, that isolation is an abstract term and that it cannot help us, therefore, in visualizing the forces inhibiting the growth of the buds while the plant is intact. We will show in a simple example that the conception of isolation, while it may fit some cases, will not fit others.

The following experiment was often repeated during the winter months. Three leaves of the same plant of *Bryophyllum* were suspended in an aquarium saturated with water vapor, so that the tips of the leaves (or about one-half of each leaf) were submersed in water at the bottom of the aquarium (figs. 1, 2, 3). Leaf 1 was completely isolated from the stem; leaf 2 had a piece of a stem of the plant attached; and leaf 3 had in addition to a piece of the stem of the plant also the opposite leaf attached. The drawings show the condition of the three leaves after 11 days. Leaf 1 formed roots in a few days, and soon after shoots at the notches of the submersed part of the leaf. In leaf 2, as a rule, all growth from the notches was inhibited, but the bud of the stem opposite the leaf grew out very rapidly into a shoot (fig. 2, *S*). The submersed part of leaf 3 again formed roots and stems in its notches, not quite but almost as quickly as leaf 1. Experiments showed that the

[1] CHILD, C. M., Die physiologische Isolation von Teilen des Organismus, etc. Roux's Vorträge und Aufsätze. Leipzig. 1911.

result is the same if both leaves of specimen 3 are partly submersed in water; both form roots and shoots in that case.

According to the idea that isolation is the cause of regeneration, we should say that leaf 1 formed new roots and shoots because it was completely isolated; that leaf 2 did not do so (for a long time at least) because, being connected with a piece of a stem, it was less isolated. But leaf 3, which was still less isolated than leaf 2, inasmuch as it had another leaf attached to the stem, formed roots and shoots much more quickly than leaf 2 and often almost but not quite as quickly as leaf 1. The idea that isolation is the cause of regeneration is obviously inadequate in this case.



FIGS. 1–3

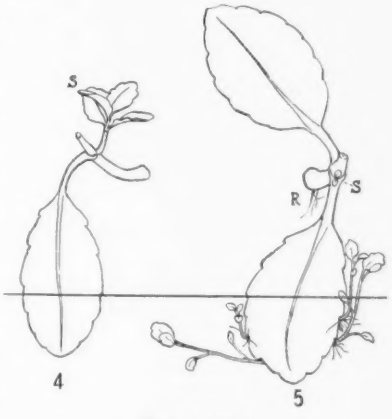
Figs. 4 and 5 are a repetition of this experiment. The two leaves had been submersed in water for 5 weeks. The leaf in fig. 4, with a piece of stem attached, had formed no roots or shoots in its notches; instead it had formed a long shoot (*S*) from the bud of the stem opposite the leaf. The leaf in fig. 5, with a piece of stem and the opposite leaf, had formed four shoots from the submersed notches, while the stem had formed one tiny shoot (*S*) from a bud in the axilla of the lower leaf, and roots (*R*) at the under side of the basal end of the stem.

When we modify this experiment and suspend the three leaves entirely in moist air (instead of submersing them partly in water), leaf 1 (entirely isolated) will again form roots and shoots in its notches; leaf 2 will as a rule show no growth, but from the opposite

bud of its stem a shoot will grow (*S* in figs. 2 and 4); and in the leaves 3 tiny roots may begin to grow from the notches which, however, usually dry up after some time; and no shoots are formed if the leaf is suspended entirely in moist air.

III. Inhibition of growth of leaves by growth of buds on stem

The question now arises: Why does the presence of the piece of main stem in fig. 2 inhibit or retard the formation of roots and shoots in the notches of the leaf, and why does the same piece of stem cease to inhibit (or why does it inhibit considerably less) when, as in fig. 3, in addition to the stem another leaf is left with it? Each node has two buds, one in the axilla of each leaf. When we use a specimen, as fig. 2, a shoot (*S*) will grow out in a few days from that bud of the stem where the leaf is removed; and this is the first growth which will occur in this specimen. The bud in the axilla of the leaf which is preserved will as a rule not grow out. In fig. 3, where both leaves are preserved, neither bud of the stem will grow out in winter.[2] Hence we notice that where a shoot grows out very rapidly from the bud of the stem, as in fig. 2, the leaf in contact with the stem is prevented or delayed in forming roots and shoots, but when no such shoots grow out from the bud of the stem (as in fig. 3), the notches of the leaf (if submersed in water) will form roots and shoots rather quickly.



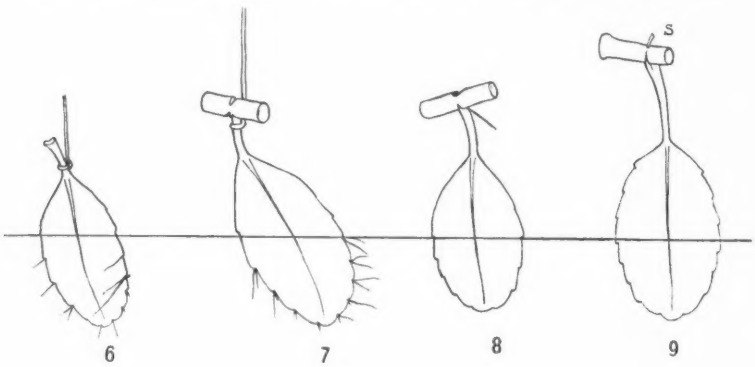
FIGS. 4 AND 5

[2] In the spring this is not so strictly true, but all these experiments were made in a greenhouse during the winter months. The greenhouse had a temperature of 70° F. or above.

The stalk of an isolated leaf without any piece of the stem is not capable of giving rise to any regeneration. Such a leaf will form adventitious roots and shoots in its notches very rapidly.

All these facts make it appear as if the growth of the buds on a piece of the stem might have an inhibiting influence on the growth of the adventitious roots or shoots of the leaf.

In order to estimate properly such an influence, an extensive series of experiments was made, in which leaves with a piece of stem attached were submersed with their tips in water, while the rest of the specimen was in moist air. In a number of stems both buds were removed (fig. 7), in another only the upper buds were



FIGS. 6–9

removed (fig. 8), while in the rest of the stems none of the buds were removed (fig. 9). If the inhibiting effect of the stem were *exclusively* due to the growth of the buds on the stem, the latter should lose its inhibiting effect entirely if these buds were removed; and the leaf connected with such a "debudded" stem should form adventitious roots or shoots as fast as a leaf without any stem. This was, however, not entirely the case. While a leaf connected with a "debudded" stem (fig. 7) formed as a rule its adventitious roots more quickly than a leaf with a normal stem (fig. 9), the leaves connected with the "debudded" stem formed their adventitious roots not quite so quickly as the completely isolated leaves (fig. 6).

Figs. 6–10 give the average results of such experiments. The drawings were made May 10, seven days after the operation. The isolated leaves (fig. 6) had all formed their adventitious roots, and so had some but not all the leaves with "debudded" stems (fig. 7). The leaves which had lost only the upper bud had not formed roots as fast as the leaves with entirely "debudded" stems (fig. 8). The leaves with normal stems (fig. 9) had not yet formed any adventitious roots, but the shoot (*S*) on the stem where the leaf had been removed had begun to grow out.

The following record of an experiment performed May 1 had yielded on May 10 the following result:

1. Completely isolated leaves (fig. 6). All ten leaves had formed adventitious roots and tiny shoots.

2. Eighteen leaves each attached to a completely "debudded" stem (fig. 7). Eleven leaves had formed adventitious roots and one also adventitious shoots.

3. Ten leaves with a stem whose upper bud was removed (fig. 8). Four leaves had formed adventitious roots or shoots.

4. Ten leaves with a normal stem (fig. 9). All these stems formed shoots from the upper bud. No leaf has formed adventitious roots or shoots.

It is, therefore, obvious first that a stem whose buds are removed has still an inhibiting influence upon the formation of roots in the notches of a leaf; and second, that if the buds of the stem are not removed the growth of the bud opposite the leaf enhances this inhibiting effect of the stem upon the leaf considerably.

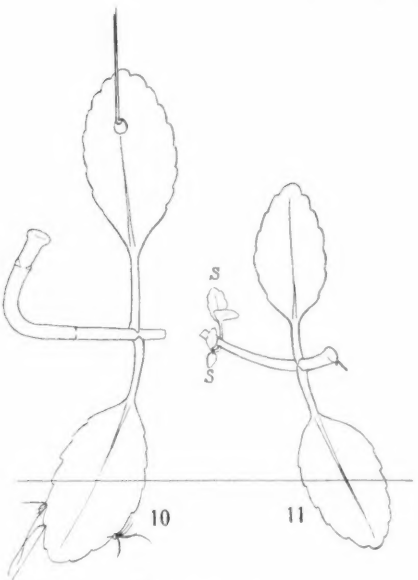
Since the growth of this bud of the stem is as a rule also inhibited when the opposite leaf is not removed, as in fig. 3, we understand why the non-removal of this leaf favors the growth of the adventitious roots from the notches of the other leaf.

We have seen that isolated leaves when suspended *in moist air* will form roots and shoots from their notches even if they are not submersed in water; while if a leaf is connected with a stem, the formation of roots and shoots in the notches will be permanently inhibited *in moist air*. It should be added, that the leaves attached to a "debudded" stem may form very short adventitious roots when suspended in moist air (instead of in water), but will not

form long roots or shoots as will the completely isolated leaf. The analogy between the effect of the non-removal of the opposite leaf from the stem and of the removal of the opposite bud seems thus pretty complete.

IV. Continuation of these experiments

We have thus seen that the growth of buds on the stem is one factor which inhibits or delays the growth of the notches in the opposite leaf. We intend to show the influence of this factor in some further observations.

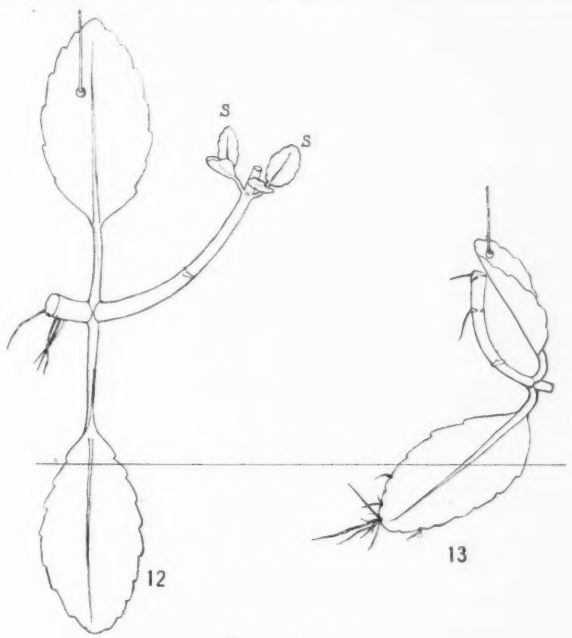


FIGS. 10 AND 11

In all previous experiments we had cut out from a plant a piece of stem with only one node. If we cut out a piece of a stem containing two or three nodes (figs. 10, 11, 12, 13) and preserve one pair of leaves, the behavior of these leaves will be different if they are left in the apical or in the basal node of the piece. Figs. 10–13 illustrate this difference. In all cases one or both leaves are partly submersed in water, while the rest of the preparation is suspended in moist air. In such cases new shoots (*SS*) were formed in a few days from the two apical buds of the stem in fig. 11, where the apical leaves had been removed and only the basal leaves left; while in specimens like fig. 10, where the apical leaves were left, the buds on the stem either formed no new shoots or formed them with some delay. As a consequence, we notice that in fig. 11 the submersed leaf formed at first no shoots, while the submersed leaf in fig. 10 in

about 50 per cent of the cases formed roots and shoots in its notches rather rapidly. This happened often, but not always, when the formation of shoots on the stem itself was long delayed. Ultimately all the leaves may form adventitious roots and shoots in the notches that are under water or near the edge of the water.

This experiment, therefore, supports the conclusion that if the buds of the stem grow out very rapidly, their growth inhibits or



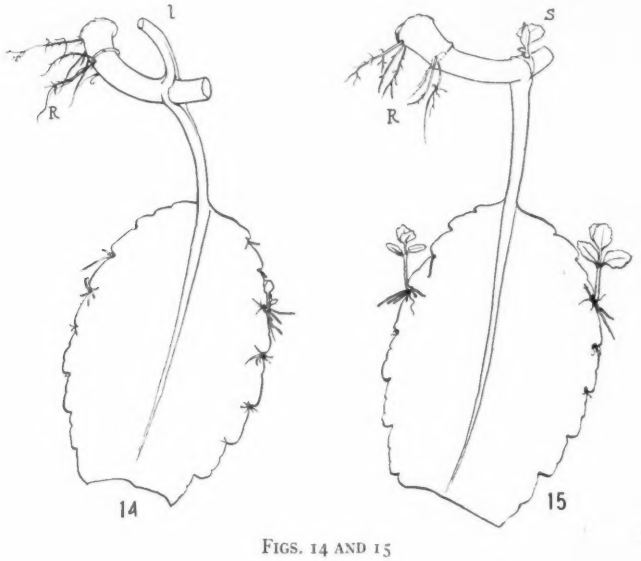
FIGS. 12 AND 13

delays the growth of roots and shoots in the notches of the leaf attached to the stem.

Figs. 12 and 13 are a repetition of the same experiment. The drawing was made 17 days after the beginning of the experiment. The stem in fig. 12 formed rapidly two shoots (*SS*) from its apical buds and this inhibited the growth of roots and shoots in the submersed leaf; in fig. 13 the stem formed no shoots and the submersed leaf could form roots. The root formation in both stems

was about equal. These experiments have been repeated so often that they can be asserted to form reliable demonstration experiments, during the winter months at least.

We have already stated that in a completely isolated leaf (as in fig. 1) the roots in the notches in the leaf do not begin to grow until a few days after the bud in a stem (*S* in fig. 2) has begun to grow. It would seem, therefore, that we might weaken the inhibiting influence of a piece of stem, as shown in the experiment in fig. 2, if



FIGS. 14 AND 15

we inhibit or retard the shoot formation of the bud on the stem. This can be done, as we have already stated, by not removing the other leaf on the stem, as in fig. 3. It is not necessary, however, to leave the whole leaf attached to the stem; it suffices if we leave a piece of the stalk of a leaf attached as in fig. 14. In this case a leaf (with a piece of stem and a piece of the stalk *l* of the other leaf) were suspended November 12 in moist air. The bud in the axilla of the stalk *l* was by the presence of the latter prevented from growing out, and after some time roots (*R*) were formed at the basal

end of the stem. Still later, roots and shoots began to grow out from the notches of the leaf (although this was not submersed in water). Fig. 14 was drawn January 18, therefore 9 weeks after the beginning of the experiment. About a week after the drawing was made, the stalk *l* which had wilted fell off and now the bud in the axilla of the stalk *l* was able to grow and the shoot *S* was formed (fig. 14). The drawing (fig. 15) was made when the shoot was one week old. The experiment shows also incidentally that the *root* formation on the stem does not (under the conditions of this experiment) inhibit the formation of roots and shoots on the leaf. We shall return to this fact later.

In this experiment the leaf was merely suspended in moist air and yet shoots developed from the leaf although it was attached to a piece of stem. This is unusual, since in order to obtain such a result with certainty it is necessary to submerse part of the leaf in water.

V. Inhibiting influence of roots on the growth of the notches of a leaf

A piece of stem when cut from a whole plant of *Bryophyllum* is not only able to form shoots but it also forms roots, and it is now our intention to consider the influence which the root formation of the stem has on the growth of the notches of a leaf. WAKKER, DEVRIES,[3] and GOEBEL[4] all have reached the conclusion that it is the presence of the main root or the regenerated roots on the stem which prevent the growth of adventitious roots or shoots on the leaf. If we break or cut off a leaf of *Bryophyllum calycinum* from the stem, neither the stalk nor the base of the isolated leaf has the power of forming roots, and this inability of root formation is considered by WAKKER and DEVRIES to be the cause of the growth of the notches. "According to WAKKER the organic separation of the leaf from the rooted part of the plant acts as a stimulus upon the leaf and induces the growth in the notches."[5]

[3] DEVRIES, HUGO, Jahrb. Wiss. Bot. **22**:35. 1890.

[4] GOEBEL, K., Einführung in die Morphologie der Pflanzen. Leipzig, 1908 (pp. 142–149).

[5] DEVRIES, HUGO, *loc. cit.* The writer was not able to obtain WAKKER's monograph.

DEVRIES describes a very striking experiment which supports the idea of WAKKER that the root of the main plant is the factor which inhibits the growth of the notches in the normal plant.

The apices of six plants were cut off beneath the most vigorous adult leaf and planted in soil. After strong roots had been formed (in the soil) their stems were cut above the lowest pair of leaves, the apices removed, and this lowest pair selected for the experiment. Both leaves were put flatly on moist sand, the one after having been removed from the stem, while the other remained connected with the roots. The axillary buds were destroyed. After three weeks the isolated leaves had formed numerous young plants on their margin. The leaves which had remained connected with the rooted piece of stem had formed no plants in their notches (and did not form any afterward), although they had otherwise been exposed to the same conditions as the isolated leaves.

This experiment is in harmony with the view that the normal roots of a stem (if they are under normal conditions) inhibit the growth of notches in the leaves. DEVRIES reports a second experiment in favor of the view of WAKKER. He cut the stem of a plant in its internodes and thus isolated seven pairs of leaves.

From each pair one leaf was broken off; all axillary buds were destroyed. The leaves were now put on moist sand. After a month the seven stems had formed roots. The isolated leaves[6] had formed in their notches rooted plantlets, varying from 10 to 26 in number. The leaves whose stems had formed roots behaved differently. One leaf had formed no trace of growth in its notches; it was the one whose stem had formed roots first. The rest of the leaves had formed only a few plants whose number varied between 2 and 6. They reached only a few mm. in length, while those of the isolated leaves measured from 0.5 to 2 cm.

We see here that if a root is formed on a stem before the roots in the notches of a leaf can grow out, the root (under proper conditions) may inhibit the growth of the notches of a leaf.

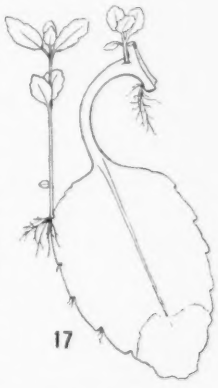
While these facts leave no doubt that the root (under proper conditions) can inhibit the growth of the notches in the leaves of *Bryophyllum*, the experiments mentioned on the previous pages of this paper show that this is not the only factor. A piece of stem, even if it does not form any roots but only a shoot, will inhibit or greatly delay the growth of the notches of a leaf connected with it.

[6] That is, those broken off from the stem.

VI. Influence of root formation and of root pressure

DEVRIES assumes with WAKKER that it is not the root formation in itself by which the stem or main plant inhibits the growth in the notches of a leaf, but the root pressure. GOEBEL is inclined to think that it is the root formation in itself, regardless of the root pressure (or flow of water caused by it), which inhibits the growth in the notches of the leaf. The writer has made a number of observations which indicate that of the two views that of WAKKER and DEVRIES is better supported by the facts.

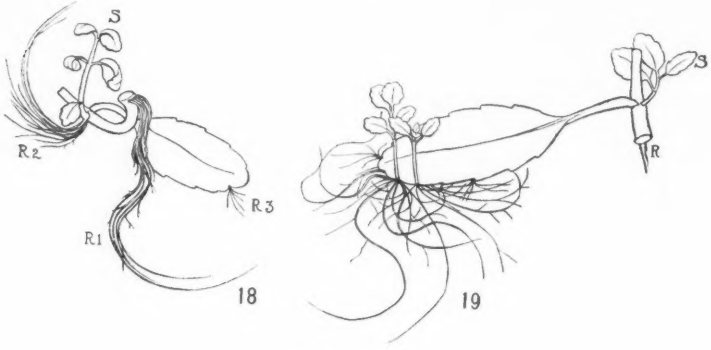
As an illustration, we may take figs. 14 and 15, in which a leaf with a piece of stem was suspended in moist air. The basal end of the stem formed a mass of roots, yet this did not prevent the growth of roots and shoots from the notches of the leaf. This contradicts GOEBEL'S assumption, but is in harmony with the view of DEVRIES, since these roots in the air were not able to give rise to "root pressure."



FIGS. 16 AND 17

As a further support, we may give the drawings (figs. 16 and 17). In these cases the leaves were cut off with only a fragment of the stem attached, which was a little larger in fig. 17 than in fig. 16. The axillary bud was not removed. The leaves were suspended in moist air. Although the remnants of the stems formed roots, yet the leaves formed also roots and shoots (although they were in moist air). The root formation on the remnant of the stem preceded the root formation on the leaf but did not prevent the latter. The experiment shows again that mere root formation in a stem suspended in moist air does not prevent the formation of roots and shoots in a leaf of *Bryophyllum*. It should be pointed out, however, that the shoots grew out from the axillary bud of the leaf; it is the growth of the opposite bud which has the inhibitory power on the leaf mentioned in the third and fourth sections.

While the root formation on the stem does not inhibit the shoot formation on the leaf if the root is exposed to moist air, the result is different if the roots are in water. If one leaf with a piece of stem (fig. 18) is put into a Petri dish, the bottom of which contains a thin layer of water, the stem will form enormous roots (R_1) at its basal end from the callus, and R_2 from the basal end of the shoot (S) which grows out from the bud of the stem where the leaf was removed. On the other hand, the leaf has formed only a few small roots (R_3) at one notch. (As a rule the notches of the leaf formed no roots in such an experiment.) In this case the roots of the stem which were functioning, and probably established the



FIGS. 18 AND 19

usual root pressure, inhibited for a long time and in most cases permanently the regeneration in the leaf.

If, however, we do not put the leaf immediately after it is cut from the plant into the Petri dish but suspend it first in moist air, the stem will form a shoot (S in fig. 19). Roots (R) may or may not be formed on the stem, but they will always be formed considerably later than the shoot, at least in winter. If after a month we put the leaf into a Petri dish, while the stem remains in moist air, the leaf (fig. 19) will rapidly form roots and shoots. The contrast between the behavior of the leaves in this case and the one mentioned before is very striking. In the experiment represented in fig. 19, the roots (R) at the base of the stem could not establish

a flow of water in the stem and could not inhibit the growth of the shoots in the notches of the leaf; and by the time the leaf was put in water they were obviously not in a position to produce a flow or a root pressure.

Roots formed on the stem have as a rule, therefore, an inhibiting effect on the growth from a leaf if they can produce a root pressure, that is, if they are in water. The formation of a shoot from the bud of a stem can produce such an inhibiting effect upon the opposite leaf if the shoot is in moist air and if no root is formed. This influence of roots on the growth of the notches of a leaf was discussed only for the sake of completeness, since it does not strictly belong to our problem, which deals only with the growth of shoots.

VII. The conditions inhibiting and accelerating the growth of the axillary buds

Each node of *Bryophyllum* has one pair of leaves, and in the axilla of each leaf is found a bud which in the normal life never grows out, but which may grow out as a consequence of a mutilation of the plant.

If we cut through two successive internodes of a stem and isolate a single node, and if we remove the two leaves, the two buds on the stem will grow out rapidly (if we provide the necessary water supply or if the node was cut out from near the base of the stem).

If we remove only one instead of both leaves, only one bud will as a rule begin to grow, namely the one whose leaf is removed. This suggests the idea that the leaf, while favoring the growth of the opposite bud, inhibits the growth of its own axillary bud. If we remove neither of the two leaves, in many cases (especially in winter) neither bud will grow out, a fact which harmonizes with the assumption that each leaf suppresses the growth of its own axillary bud.

The following experiment, however, restricts this last assumption that each leaf will inhibit the growth of its axillary bud. If we isolate a node with its two leaves (which we do *not* remove), and if we split the piece of stem longitudinally, we obtain two leaves, each attached to a half of a node containing the axillary bud of the leaf (fig. 20). In this case the axillary bud will grow out,

although often with some delay. Hence the leaf in this case does not prevent the growth of its own axillary bud, and if we speak of an inhibition in the previously mentioned cases, we have to add the remark that this inhibition only exists if the other leaf or the opposite bud are in connection with the first leaf. A comparison of figs. 20 and 21 is of interest. In both cases leaves with a piece of stem attached were suspended in moist air on February 20. They were drawn on April 1. In fig. 20 the shoot (*S*) in the axilla of the leaf left attached to a longitudinally split piece of stem grew out. In fig. 21, one leaf with a whole, non-split piece of stem attached gave rise to the growth of the shoot (*S*) on the upper side of the stem where the leaf was removed, while the bud in the axilla of the leaf was prevented from growing.

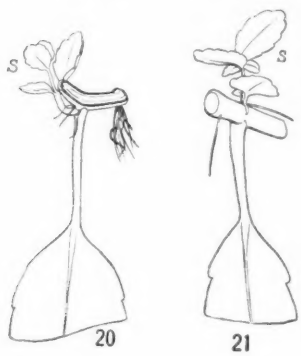


Fig. 22 is a case similar to fig. 14, one leaf with a piece of stem and the stalk *l* of the opposite leaf. In this case the bud (*S*) in the axilla of the intact leaf grew out. This is not the most common experience. More often in winter neither of the two axillary buds of the stem will grow out under such conditions. The experiment in which the piece of stem is split longitudinally (fig. 20), however, generally succeeds.

FIGS. 20–22

The following observation is also of some significance. If we cut out a node, remove one leaf and its bud, but preserve one leaf and the bud in its axilla, the latter will grow out into a shoot after some delay. Hence the removal of the opposite bud removes the inhibiting influences which this bud naturally has on the growth of the bud in the axilla of a leaf. We can accelerate the growth of this latter bud, however, when in addition to the removal of the opposite bud and leaf we make an incision or cut out a piece from the rind apically to the axillary bud whose leaf is not removed. In

this case the bud in the axilla of a leaf which is not removed will grow out rather rapidly.

We may anticipate that all these experiments indicate that the growth of the bud depends upon the flow of certain substances from the leaf to the bud. That bud which receives these substances first will grow out first, and thereby prevent the flow to the other bud whose growth is thereby "inhibited." The apparent inhibition of growth in one place is simply due to the fact that under the conditions of the experiment the substances required for growth flow to some other place and are retained there, and the removal of the inhibition consists in creating conditions which will force the substances to flow where we want growth to occur.

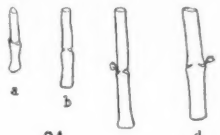
VIII. The rules and mechanism of inhibition in regeneration

We cut off the base and tip of the main stem of a plant of *Bryophyllum*, remove all the leaves, and suspend the stem in a closed aquarium saturated with water vapor. Only the two buds at the highest apical node will grow out (fig. 23); it does not matter whether the stem is hung upright or inverted. The buds at the more basal nodes are all inhibited from growing by the growth of the two apical buds; for if we isolate any of the lower nodes, their buds also may grow (fig. 24). This is the well known example of an inhibition of one part by another. In the terminology of REINKE, we might call the two apical buds the "dominants." What is the source of their dominance? By way of an answer we intend to show that the following relation exists: *If an element a inhibits the growth in an element b, b very often accelerates or makes possible the growth in a.* When we cut off a single node near the top of the main stem of *Bryophyllum*, remove the two leaves, and suspend it in an aquarium saturated with water vapor, as a rule the two buds will not grow out. If, however, we leave it in connection with one or more of the lower nodes of the stem, it will regenerate, and incidentally inhibit the growth in the lower nodes (figs. 23, 24). The regeneration and growth of the two shoots at the apical node will as a rule be the quicker the more nodes are left in contact with it. Hence the lower part of the stem whose regeneration is inhibited by the apical node, at

the same time accelerates the latter's regeneration or makes it possible.

The second example is the following: When we cut off one leaf with a piece of the main stem (as in fig. 2) and suspend it in water, the bud opposite the intact leaf will grow out into a shoot (*S* in fig. 2). We have seen that the growth of this shoot has a share in the inhibition of the growth of the notches of the leaf in this experiment. It can be shown that conversely the leaf accelerates or renders possible the growth of the bud in the stem. As stated, the isolated node near the top will not be able to form shoots if suspended in moist air. If, however, one leaf or even a fraction of one leaf is left in connection with the stem, the bud on the opposite side will grow out (figs. 25–29). In the isolated nodes (figs. 28, 29) cut off near the apex no buds could grow in moist air. When, however, only a piece of a leaf was left in connection with such a stem, as in fig. 25 or 26, the bud could grow out. Here we see again that the presence of the leaf accelerates or renders possible the growth of that shoot in a stem whose formation inhibits or retards the growth of the notches of the leaf.

23



FIGS. 23 AND 24

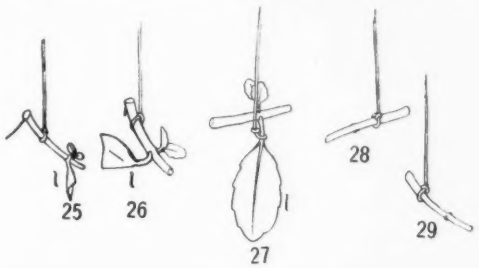
This gives us a clue to the nature of the dominance and the power of inhibition. The inhibition seems to consist in this, that the dominant part receives something from the inhibited part which accelerates growth or renders it possible in the former.

When we put an isolated node from near the top (whose leaves are removed and which cannot regenerate in moist air) in a very thin layer of water, new shoots grow out (figs. 30–32). This looks as if the "something" which the inhibited part supplies to the dominant part were water. But the writer is suspicious that the water may be only indirectly needed, namely to render the flow of material in the conducting vessels possible. In animals we know that the blood vessels must be filled to render a closed circulation possible. It would seem as if in plants a flow of substance through

conducting vessels should be possible only if a certain minimum amount of water is contained in the conducting cells or vessels.

The buds of an isolated node nearer the base of the stem may grow out if suspended in moist air, probably because such a piece does not dry out so easily.

The following experiment rarely fails. If we suspend a piece of stem consisting of several nodes and stripped of all leaves in moist air (fig. 33), the two most apical buds (*b*) will grow out. Their growth, which is usually slow, is greatly accelerated if we leave one leaf (or more) on the stem (*b* in fig. 34). In two weeks the growth of the apical buds (*b*) in fig. 33, which had no leaves, was very slight, while it was strong in the stem (fig. 34) in which one



FIGS. 25–29

leaf was left. Here we have the combined accelerating effect of stem and leaf upon the growth of the apical bud.

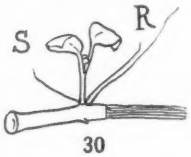
Why is it that the apical bud grows out first? Should this be connected with the anatomy of the conducting vessels, possibly in the way that the majority of these vessels go directly from the leaves to the growing point at the apex?

Since the rapid growth of the bud on a stem inhibits or retards the growth of adventitious roots of the opposite leaf (fig. 2), it follows that the removal of the bud or the inhibition of its growth should favor the growth of adventitious roots in the notches of the leaf. This is indeed the case. If we suppress the growth of the two buds in an isolated node, we favor the growth of adventitious roots in the leaves if they are submersed in water (fig. 3). The same happens if we split the node longitudinally (figs. 35, 36). The leaf

(fig. 35) connected with a longitudinal half of a node was submersed in water and formed adventitious roots in nine days. The leaf (fig. 36) attached to a whole node formed no adventitious roots under the same conditions.

IX. Isolation, inhibition, and the flow of material through the plant

These rules give us some basis on which we may try to form a preliminary idea on the nature of the mechanism of inhibition. As we mentioned already, the rules are comprehensible if we assume a flow of certain (possibly specific) substances (or formed cells) from the places where the dormant buds are ready to grow, or the prevention of such a flow toward these dormant buds.



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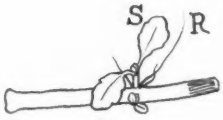

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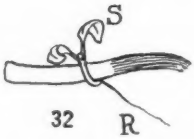


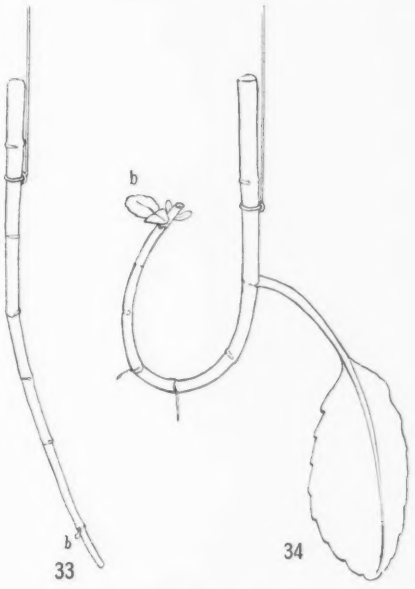
FIGS. 30–32

We will first show in a few simple examples that this idea leads us easily through the maze of facts in which the terms isolation or inhibition have no more than a metaphorical value.

When we isolate a leaf and suspend it in moist air or put it into a Petri dish the bottom of which is covered with water, as a rule only a few of the notches will grow out into shoots. Why do not all grow out? From what was said in the previous section it was natural to expect that the growth of the shoots in some of the notches of a leaf inhibits the growth in the rest of the notches of the same leaf, and that if all the notches could be isolated from each other this inhibiting effect would cease and they would all grow out. This idea was put to a test in a way indicated in fig. 37. Five notches on one side of a leaf were isolated from the leaf and from each other. The rest of the leaf and the isolated notches were put into a Petri dish whose bottom was covered with a layer of water. All five isolated notches grew out into shoots, while only three of the ten or twelve notches left on the leaf grew out. This

experiment, which has often been repeated, succeeds easily if the piece of leaf left around each notch is not too small. It is noticeable that the rapidity of growth is greater in shoots which grow out from a whole leaf than in those growing out from the isolated notches. Here we see again an application of the rule that if an organ *a* inhibits the growth in *b*, the presence of *b* accelerates the growth in *a*. This is intelligible on the assumption that the leaf furnishes a flow of liquid containing material for the growth of shoots; and that the flow of this material away from the notches (wherever this may be) leads to the inhibition of the growth in the notches.

When the piece of leaf around an isolated notch is too small, no growth may occur or only tiny roots or shoots will grow out. This observation again agrees with the assumption that a notch of a leaf will grow into roots and shoots if certain substances or formed constituents of the leaf flow toward a notch or are prevented from flowing away.

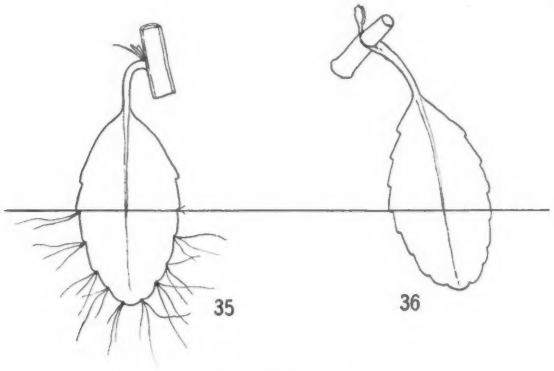


FIGS. 33 AND 34

We can understand the experiment illustrated in fig. 37 on the assumption that if in a leaf one or more notches begin to grow out into roots and shoots, these shoots determine a flow in the rest of the leaf in a similar way as if a piece of the stem had remained attached to the leaf; and with the same inhibitory or retarding effect upon the growth of the other notches of the leaf. If, however, each notch is isolated and given enough water (for example, if

it is put into a Petri dish which has a very thin layer of water), each notch can grow out, since the inhibitants through the establishment of currents in the leaf to growing shoots are lacking.

We have stated that if a leaf is suspended in moist air the growth of the shoots is prevented if a piece of a stem is left attached to the leaf. It seemed of interest to find out if this inhibiting effect would show itself even in a leaf in which a number of lateral incisions were made. This is indeed the case, as figs. 38 and 39 show. In these experiments the incisions were such that the pieces of the leaf had to be kept together by stitches of a thread. The leaves were suspended in moist air. Yet complete inhibition of the growth of



FIGS. 35 AND 36

the notches occurred in the leaf which was connected with a piece of stem (fig. 38). If a flow of substances from the leaf to the piece of stem is the cause of inhibition, such a flow must have taken place along a zigzag path in the leaf. One finds occasionally in such an experiment that in the extreme apical piece of the leaf the inhibiting effect of the stem may cease and that there a growth of roots may occur in the notches.

That the flow of water and of the material it carries in a stem may be deviated and altered by the growth of new shoots is rendered obvious by such observations as are represented in figs. 40 and 41. In this and similar cases thick pieces of the stem of *Bryophyllum*

were cut out from the plant, deprived of their leaves, and put on moist soil. As is usual, shoots grew out very soon from the top buds of the stem; very soon afterward the piece in front of the top node began to shrink and wilt, not directly to the top node, but to within a few millimeters (fig. 40). When by chance the new shoot grows out not from the top node but from the one next to it, the whole piece in front of the top node may wilt (fig. 41).

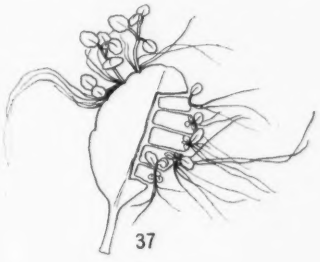
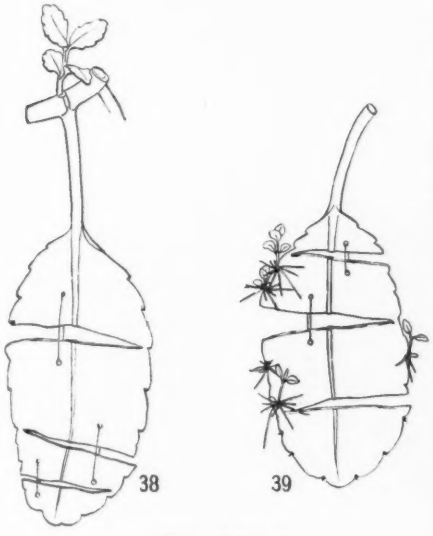


FIG. 37

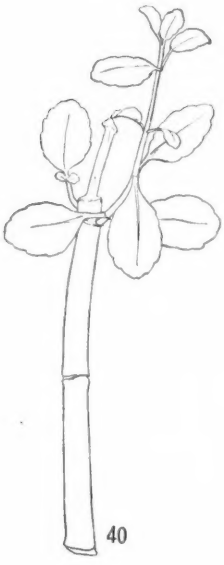
These observations were made on stems kept in the laboratory rooms (not in the greenhouse). When the root of the stem is left intact and in its natural position, this wilting of the piece of the stem in front of the node from which the new shoots grow out will not occur. The ascending flow of liquid or material in the stem was deflected in this experiment into the most apical bud, and there was not enough root pressure to maintain a flow through the pieces of the old stem more apical than the new shoot.



FIGS. 38 AND 39

By way of parentheses we may here briefly mention that light exercises a great influence on the growth of the notches of an isolated leaf. If such leaves are suspended in moist air but free from light, as a rule none of the notches will grow out, while they will grow out

promptly as soon as they are exposed to the light; provided they had not been kept too long in the dark. If the leaves are kept in the dark in a Petri dish whose bottom is covered with water, a few notches may grow out, but they are not nearly as numerous as



FIGS. 40 AND 41

those growing out in the light. Whether we are dealing here with a direct chemical effect of the light or with an indirect effect on the flow of substances in the leaf remains to be seen. It should not be overlooked that as soon as the leaves of *Bryophyllum* turn yellow they become less turgid and easily fall off from the stem.

X. Theoretical remarks

We may now go back to the first experiments mentioned in this paper and try to analyze them on the basis of the old idea that the flow of material in the plant is responsible for phenomena of growth. We start from the assumption that a notch of a leaf can

grow out only if there is no flow of liquids (carrying non-formed or possibly formed material) away from the notches. This is not the case in the normal plant when the circulation is normal, and WAKKER and DEVRIES have shown the rôle which the root pressure plays in this case. But the root pressure is not the only factor which influences this flow. The experiments in figs. 1–3 seem to indicate that different factors aside from the root pressure can determine the flow away from the notches of the leaf, provided our assumption is correct that such a flow is the cause of the phenomena of growth and regeneration observed.

If we go back to these first experiments in this paper and try to formulate them in harmony with this idea, we should have to state that in a completely isolated leaf the flow away from the notches ceases. As a consequence, one or more of the notches may grow out, and as soon as this happens the flow in the leaf is directed toward the growing notches. They act as if they exercised a "suction" on the flow of liquids in the leaf, and they may inhibit the growth in other notches of the leaf.

If the leaf is in connection with a piece of stem, the latter exercises this "suction," and the flow of liquids is away from the leaf to the stem; hence the inhibiting effect of the stem upon the growth of the notches of the leaf. This "suction effect" is especially great if the bud opposite this leaf can grow out, as in fig. 2. If both leaves are left attached to the piece of stem (as in fig. 3), the flow from a leaf will be deflected from the buds and may go into the opposite leaf. This might explain why when both leaves remain attached to a piece of stem the growth of the notches of the leaves is favored again, though it is not so rapid as in a completely isolated leaf.

This idea of a deflection of the current away from the leaf toward the opposite side of the stem is in harmony with the fact that the bud opposite a leaf grows out very quickly if its own leaf is removed (fig. 2); while the growth of the axillary bud of the leaf which is not removed is inhibited in this case. If we split the stem longitudinally, this deflection ceases and the leaf ceases to inhibit the growth of its own axillary bud. This idea is supported by the fact that if the leaf attached to a longitudinally split node is partly suspended in water its notches will grow out rather rapidly.

We have assumed that if we have a node with its two leaves attached, the flow will be deflected from the buds; this again is in harmony with the facts that in such a case as a rule neither of the buds grows out.

When a plant is normal, it is almost or possibly absolutely impossible to induce the notches of a leaf which is connected with the plant to grow. The writer has submersed such leaves in water, but in months not a single notch ever formed a root or a shoot. If, however, the flow of substances in a plant is abnormal, either because the roots or the apical parts or both have suffered, a growth of shoots may occur in moist air from the notches of leaves which are in contact with the plant. This fact is mentioned by DEVRIES and is well known to those who have seen the plants in their natural conditions in Bermuda.

If we now return to the question from which we started, namely, why it is that the notches of the leaves of *Bryophyllum* will not grow out while in connection with the normal plant, the answer should be that the flow of material from the root and from the leaves into the stem and to the apical end of the latter prevents this growth. Through this flow material is carried away from the notches of the leaves. The anatomy of the conducting vessels and tissues, which is inherited, and the dynamical factors determining the flow are the factors concealed in the term "correlation." We understand why it is that if we isolate a part, buds may grow out which without the isolation would not have grown, the reason being that in the mutilated part material can flow to and be retained at places where if the part had remained in the whole it could not have been retained. This assumption agrees with the older ideas of DUTROCHET, SACHS, DEVRIES, and GOEBEL on regeneration in plants. We understand on this basis why it is that the term isolation of parts or the inhibiting effect of growing parts on others may express some but not all the facts of regeneration. It is not the isolation in itself, but the retention of material in places where there would not have been such a retention under ordinary conditions which apparently determines the growth of dormant buds in an isolated piece; and so it may happen that while this term expresses adequately some results, it fails in others.

SACHS assumed that specific organ-forming substances were needed for growth, and that the consumption of these substances in the growing regions was the cause of the inhibition of growth in the dormant buds of a plant. While the first half of the theory may be correct, the second part is not tenable, since in each stem of a *Bryophyllum* there is enough "formative" material to allow each bud in all the nodes to grow out, while as a matter of fact only the most apical ones will do so. This is intelligible on the assumption that these apical nodes retain the "formative" material in excess of what they need for their own growth.

The ideas expressed in this paper agree in the main with the results and conclusion of the author's older experiments on regeneration in animals. The writer had found that if a piece be cut out from a stem of a *Tubularia* a new polyp may form at each end of the stem, but that the formation of the polyp at the oral end precedes that at the aboral end; and the difference in time may be from one or two days to as many weeks, according to the species or the temperature. He found also that the formation of the oral polyp is the cause of the delay in the formation of the aboral polyp, and that if he prevented the formation of the oral polyp this delay in the formation of the aboral polyp was no longer observed.[7] This is the same rule which we have found for the relation between the growth of the bud of the stem and the formation of adventitious roots and shoots in the opposite leaf of *Bryophyllum*. The growth of this bud causes a delay in the growth of adventitious roots and shoots in the opposite leaf, and this delay is suppressed or diminished if the bud is prevented from growing.

The writer suggested that a flow of substances was the cause of these phenomena of correlation in *Tubularia*. He had found that pigmented cells which come from the entoderm and are carried in the circulation are always collected at the spot where regeneration of the natural growth of the hydroid is to start.

These remarks may suffice to indicate that the rules of inhibition observed in *Bryophyllum* may have a wider application.

[7] LOEB, J., Untersuchungen zur physiologischen Morphologie der Tiere. I and II. Würzburg. 1890 and 1891; Pflüger's Archiv **102**:152. 1904.

XI. Summary of results

The phenomena of inhibition of regeneration have been studied in *Bryophyllum calycinum* and it was found that they are governed by the following simple rule:

If an organ *a* inhibits the regeneration or growth in an organ *b*, the organ *b* often accelerates and favors the regeneration in *a*.

This rule is best understood on the assumption that the inhibiting organ receives something from the inhibited organ necessary for regeneration.

It is pointed out that this harmonizes with the older assumption of botanists and of the writer that the flow of material and the block to such a flow after mutilation is responsible for the phenomena of inhibition in regeneration, as well as for the phenomena of correlation.

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NEW YORK CITY

VASCULAR ANATOMY OF THE MEGASPOROPHYLLS OF CONIFERS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 208

HANNAH C. AASE

(WITH 196 FIGURES)

Introductory and historical

The megasporophyll in Coniferales has been the subject of much investigation and discussion, as on the interpretation of this structure depends to a great extent the views held in regard to the relation of living conifers to fossil forms, and the interrelation of living genera. If the scale in *Pinus*, the ligule in *Araucaria*, and the epimatium in *Podocarpus* represent a dorsal outgrowth of the bract, there is added a strong argument in support of the contention that the conifers have sprung from lycopod stock. If the megasporophyll represents a metamorphosed fertile shoot and its subtending bract, there exists a suggestive likeness to the Cordaitales, in which the presence of bracts on the shoot makes its identification as a shoot less difficult. Again, if the scale in the Abietineae represents an axillary shoot and the ligule in *Araucaria* represents a dorsal outgrowth, two other possibilities may be suggested: either the Coniferales have a double origin, or the Cordaitales included not only forms with compound strobili in which the scale is a metamorphosed structure, but also forms with simple strobili in which the scale is a ligular outgrowth of the bract. All these four views are supported by various investigators. Correlative with the views taken as to the origin of the group as a whole are the views as to the interrelation of genera; forms which may be considered as progenitors according to one theory may be the descendants according to another, or there may exist no relation.

The investigators before 1868 were concerned chiefly with gross observations of development and abnormalities. Rather

complete summaries of these investigations are given by RADAIS (2) and WORSDELL (11).

VAN TIEGHEM (9) in 1869 was the first to attack the problem from the standpoint of vascular anatomy. He studied forms from all the six large groups. He concluded that the megasporophyll in all Coniferales is a compound structure. The seminiferous scale represents the first and only leaf of an axillary shoot, as the vascular supply to the scale is arranged in an arc. The ovules are borne on the dorsal side of the leaf except in *Araucaria*, where the ovule is reflexed toward the ventral side and hence appears to be located between the bract and scale. In the Podocarpineae and Taxineae the leaf is reduced to such an extent that it is represented practically only by the ovule. In *Podocarpus* the leaf is folded on its dorsal surface to form an anatropous ovule, while in *Pherosphaera*, species of *Dacrydium*, *Phyllocladus*, and the Taxineae, the leaf remains erect and the ovule is orthotropous. The inversion of the ovule in certain forms is probably related to the greater elongation of the sporophyll beneath the ovular insertion in those forms.

STRASBURGER (6, 7) in 1872 and 1879 gave comprehensive descriptions of forms from all the groups. He held that in all cases the ovule-bearing organ is an axillary structure. In *Taxus* and *Torreya* the ovule is borne at the end of a secondary leafy shoot; in *Cephalotaxus* the secondary shoots are reduced to ovules. In the podocarps the secondary shoot is leafless and often reduced to an ovule as in *Phyllocladus*, or provided with a stalk as in *Dacrydium* and *Podocarpus*. In the Araucarineae it appears as if a stalk bearing an inverted ovule were fused to the dorsal side of the bract. In *Cunninghamia*, which he classified with the Araucarineae, there is a fusion of an inflorescence to the bract. In the Abietineae the scale is a flattened axillary structure which is folded inward and hence bears the ovules inverted. The two ovules suggest that the axillary shoot is an inflorescence, a primary and two secondary shoots similar to the two-flowered inflorescence in *Cephalotaxus*. In the Cupressineae and Taxodineae the scale and bract are fully welded together. Where many ovules occur, as in *Cupressus*, he left it undecided whether the ovules represent

a reduced branch system, or the large number of ovules is a new feature.

RADAIS (**2**) in 1894 made a rather intensive study of a number of cones of the Abietineae and Taxodineae. He notes that the bundles to bract and scale are distinct in origin in the Abietineae, *Sciadopitys*, and some of the Taxodineae, as *Cryptomeria*, *Taxodium*, and *Sequoia*, and how this distinctness is on its way to obliteration in species of *Arthrotaxis* and more so in *Cunninghamia*, and is lost in *Araucaria Rulei*.

WORSDELL (**10, 11**) in 1899 made a comparative study of types from the different tribes. He believes that in the megasporophyll in all conifers there is an axillary structure concerned. Speaking of *Araucaria* he says:

> Holding to the theory of the axillary bud as the explanation of the structure of the appendage of the cone in *Araucaria*, I believe, with CELAKOVSKY, that the ligule represents the seminiferous scale which is itself the vegetatively developed outer integument of a sporangium situated in the anterior position on an axillary bud. This outer integument has become almost completely fused with the subtending bract in *Araucaria*, completely so in *Agathis*.

Concerning the Taxeae and Podocarpeae he says:

> The Taxeae differ from the other groups in the fact that the sporangia occur in a position terminal instead of lateral to the axis on which they are borne. The anatomy points clearly to the fact that no axial foliar appendage of any kind exists upon which the sporangia are inserted, the cylinder of the axis being directly continuous into the base of the sporangium. This latter difference, however, amounts to very little if we regard, with CELAKOVSKY, the seminiferous scale of the other groups as being the morphological equivalent of the outer integument of the Taxeae, which has become, with the exception of Podocarpeae, vegetatively developed. In the Podocarpeae the relationship is precisely the same as in the Taxeae, with the exception of the axillary instead of terminal position of the sporangium. In this order the bundle system belonging to the sporangium (which is in all the other groups the sole representative of the sporophyll according to the view I here adopt) becomes obvious, owing to the fact that the latter gets by the basal intercalary growth on to the upper part of the bract. In the four other groups the bundle system pertaining to the vegetative development of their outer integuments, which, in the form of the widely expanded seminiferous scale, possesses a pronounced vascular tissue.

SEWARD and FORD (**3**) in 1906, in a somewhat extensive article on living and fossil Araucarineae, offer no interpretation of the

megasporophyll in the Abietineae, but in the Araucarineae they consider it as a simple structure which may or may not be homologous with the double structure in other conifers. They regard the Araucarineae as one of the oldest if not the oldest of the conifers. They favor the lycopod origin of the Araucarineae and set them apart under the name of Araucariales.

THOMSON (**8**) in 1909, in a paper on *Saxegothaea* and *Microcachrys*, admits that the brachyblast theory is inevitable in the Abietineae, Taxodineae, and Cupressineae. Accepting BRAUN'S conception that the scale in the Abietineae represents the first and only two leaves of an abortive shoot, which have fused by their adaxial margins, he says:

> The first inversion is explained and the ovules in the group are borne on the morphological under side. The second inversion is analogous to the single one in *Saxegothaea* and of the nature of a sporangial supply. There are then two great groups of conifers from the standpoint of this study, the simple and the complex scaled series. Both forms have the ovules on the physiologically upper surface, a position rendered almost imperative by the necessities of the seed habit. This position however has been attained in two very different ways.

STILES (**5**) in 1912 investigated several species of *Podocarpus*. He concludes that the original position of the ovule was erect and axillary as in *Pherosphaera*, but that owing to growth of the scale at the base of the sporophyll it has been carried away from the axis. As a result it has become inverted, and correlated with the inversion is probably the development of an incomplete epimatium.

> Whether this epimatium is an outgrowth of ovular or sporophyll tissue it is at present impossible to say. The evidence of development in *Saxegothaea* and *Microcachrys* suggests the former, while a somewhat older state in *Dacrydium cupressinum* suggests the latter.

In the latter form the ovule is borne on the epimatium, while in *Podocarpus* the epimatium has elongated into a stalk. The development of a strong and independent vascular supply in the epimatium he thinks is the result of a required need of a larger ovule. The epimatium in the podocarps and the scale in the Abietineae are homologous, but both are new structures. Both these complicated structures have been derived from a simple sporophyll.

The Abietineae and Podocarpineae have come from a common primitive stock. The Abietineae are more advanced in the development of the scale, but more primitive in holding on to a perfect cone. "The evidence at present is much in favor of the lycopodean ancestry of the conifers." He has little faith in the brachyblast theory, as it depends for its support mostly on abnormalities and the vascular anatomy of the cone scales. "But abnormalities, especially when they are supposed to be more or less of the nature of reversions, afford by themselves unsatisfactory evidence of phylogeny." Vascular anatomy disproves the double nature of the megasporophyll of the araucarians and podocarps, except in some species in the latter, and there the compound structure is of recent origin.

SINNOTT (**4**) in 1913 gave a very clear account of the strobilar anatomy in a number of podocarps. He is of the opinion that the podocarps and araucarians, along somewhat parallel lines of development, have been evolved from ancient abietinean stock. The scale in the Abietineae, the ligule in the araucarians, and the epimatium in the podocarps are all homologous and vestiges of an axillary shoot, and a simple sporophyll has arisen either by the fusion of both of its parts or by the abortion of one. Of the podocarps he considers those most primitive in which the epimatium is well developed and has a strong vascular supply, as *Podocarpus;* and those most advanced in which there is a reduced epimatium, as *Dacrydium*. In *Podocarpus dacrydiodes* there is a definite step in the direction of *Saxegothaea*, *Microcachrys*, and *Pherosphaera*. The resemblance in reproductive structures between certain members of the Podocarpineae and *Cephalotaxus*, the most primitive genus of the Taxineae, suggests that the latter family has arisen from some ancient member of the Podocarpineae.

EAMES (**1**) in 1913, in a paper on *Agathis*, considered also the megasporophyll situation in other conifer groups and concludes that the megasporophyll is compound in origin in all Coniferales. "Even within themselves the Araucarineae show a complete series from a form with strobilar units of a distinctly double nature to one most simple through reduction." EAMES has traced a similar reduction in the Taxodineae.

Investigation

ABIETINEAE

The ovulate strobilus in all the Abietineae is composed of a comparatively large number of sporophylls. The sporophyll here is obviously composed of two organs. In some forms, as *Ketcleeria* and *Pseudotsuga*, each of the three-pronged bracts is reflexed over the scales below, giving the strobilus a bristly appearance; while in others, as *Cedrus Libani*, the bract is a minute flap, and its bundle dies before it reaches the free portion. Between these two extremes are many intermediate forms. That the bract is a modified leaf seems evident at least in some genera. In *Pseudotsuga* and *Larix* there is a gradual transition from ordinary foliage leaves to bracts of a well developed sporophyll; and in abnormal cones of *Picea*, *Larix*, etc., the bracts are like the vegetative leaves. The scale is well developed in all the Abietineae.

The vascular anatomy of the megasporophyll is less variable in the different genera of the Abietineae than is the case in any of the other five groups.

In the lower one-third or more of the strobilus of *Pinus maritima* and *P. Banksiana* there is a general sterilization, beginning with failure of the ovules to produce seed, followed lower down by the abortion of the ovules, and finally at the base of the strobilus the reduction in size and final disappearance of bract or scale or both. In *P. Banksiana* the bract disappears before the scale, but both are finally lost, and between the lowest ovuliferous scales and the bud scales is a region where the strobilus stalk is smooth except for slight elevations (fig. 2). Each of these elevations is supplied with a small vascular strand and suggests a vestige of a megasporophyll. In *P. maritima* only the scale suffers reduction and loss, and the bract, reduced throughout the strobilus, increases in size toward the base (fig. 1).

Correlative with the sterilization and reduction of the appendages in the lower portion of the strobilus are variations in mode of origin of their vascular supplies (figs. 3–29). In the upper half of the strobilus the bract supply originates as a single bundle at the base of the cylinder gap. The scale originates as three or four bundles instead of two as in other Abietineae, one at each side of the

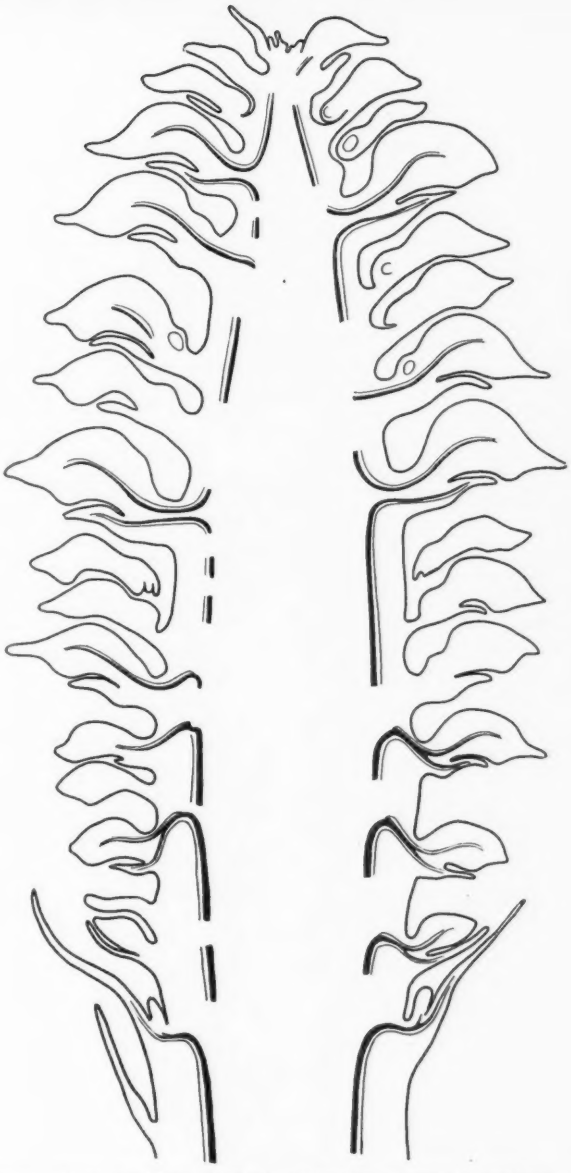


FIG. 1.—*Pinus maritima:* longitudinal section of ovulate strobilus; vascular supplies to bract and scale of each sporophyll, separated in cortex of strobilus by mass of parenchyma in upper portion, approach one another near middle and merge in lower portion of strobilus; in lower portion of strobilus scale decreases in size, while bract becomes comparatively larger.

gap some distance above the bract bundle, and above these again one at each side of gap, or one at one side only. The two uppermost

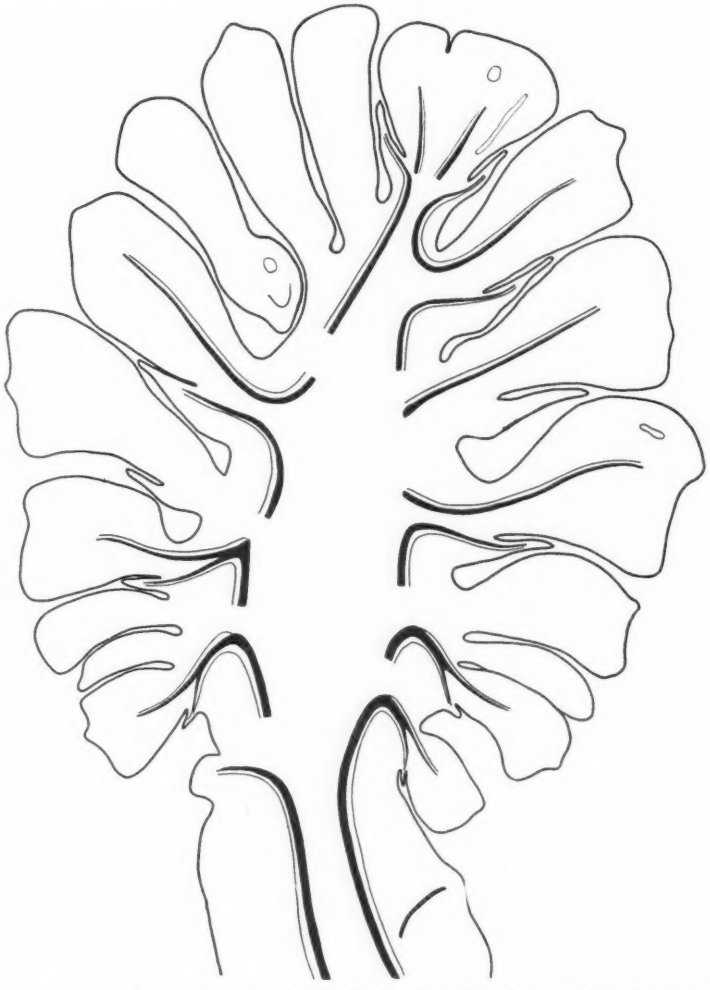
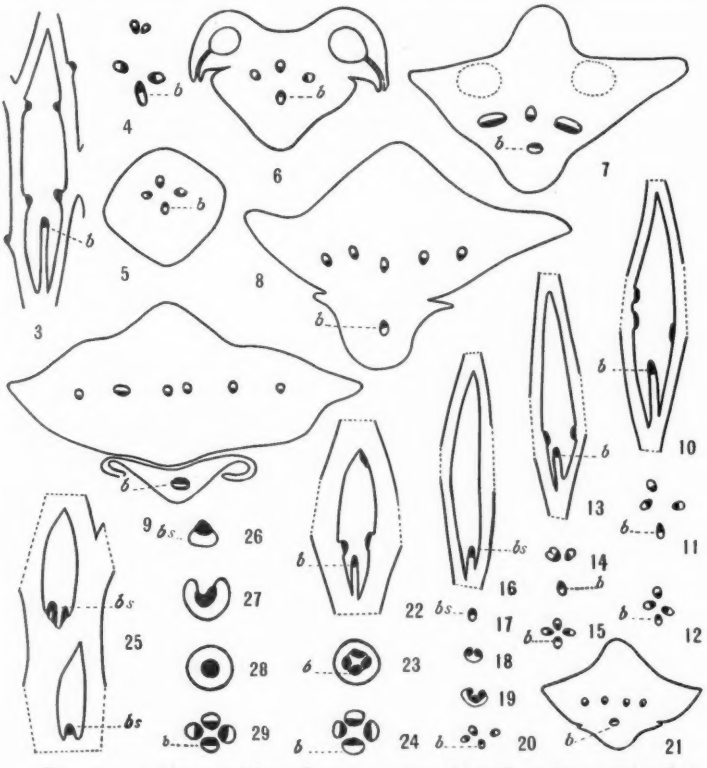


FIG. 2.—*Pinus Banksiana:* longitudinal section of ovulate strobilus; bract and scale supplies, as in *P. maritima*, separated in upper region of strobilus but become merged in lower; unlike *P. maritima*, bract becomes very small in lowest sporophylls; beneath lowest sporophylls are humps, each supplied with a bundle.

bundles soon unite into one, so that four bundles in all with xylem facing result; the lower passes undivided to the end of the bract, the three remaining spread out and give rise in the scale to a row of inverted bundles, seven or more in *P. maritima*, twelve or more in *P. Banksiana*. No branches are seen to bend toward either of the two inverted ovules. Below the middle of the strobilus the uppermost one or two bundles, as the case may be, originate near the lower scale bundles or become united with the latter so that the scale supply starts as two bundles. One of the two bundles soon divides, so that four bundles including that of the bract result; the subsequent course in the appendages is as described before. In the lower sporophyll, the scale supply originates as one or two bundles very near the bract bundle. In the lowest sporophylls the bract and scale supply originates as a single bundle at the base of the gap. In either case there is a subsequent separation into four bundles which supply their respective appendages as before described. In this region of the strobilus the four bundles remain closer together in their course through the cortex than is the case in the upper. In *P. Banksiana* the phloem is continuous around the four xylem strands, which except for a few parenchyma cells would form a solid xylem strand. Near the base of the strobilus, in this species, where the sporophyll supply begins as a single bundle, the xylem creeps around its protoxylem as a pivot and the phloem about the xylem, so that a concentric bundle results. On nearing the appendage the bundle drops into four. In this species the gaps are small, owing to a shortening of the strobilus axis. In both species the sporophyll supply takes a diagonal downward course through the cortex in the lower part of the strobilus, in contrast to the diagonal upward course taken near the tip. This is also likely due to a shortening of the strobilus axis and a consequent crowding of the appendages.

For the sake of comparison, the anatomy of a young vegetative shoot was investigated. In *P. maritima* and *P. Banksiana* (figs. 30–35), whether the bud is to give rise to a spur shoot or a long branch, a single bundle springs from the base of the cylinder gap and supplies the bract, while two other bundles, one at each side of the gap, supply the bud. The bud bundles increase in size and

divide, giving rise to a semicircle of bundles with xylem on the concave side, facing the xylem of the bract bundle. The semicircle



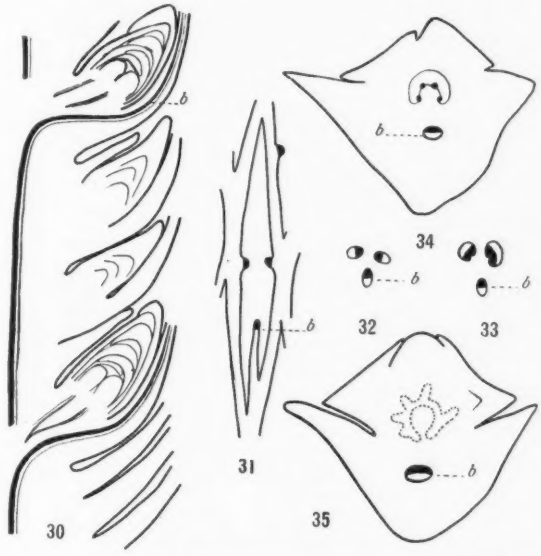
FIGS. 3–21.—*Pinus maritima:* figs. 3–9, course of bundles to bract and scale in upper half of strobilus; fig. 3, origin of bract bundle (*b*) and scale bundles (4 remaining) in strobilus cylinder; fig. 4, two upper bundles uniting; figs. 5–9, transverse sections of sporophyll, bract bundle remaining undivided, scale bundles giving rise to several bundles; figs. 10–12 and figs. 13–15, from lower half of strobilus, scale bundles decreasing in number and originating nearer to bract bundle as base of cone is approached: figs. 16–20, from lowest sporophylls, bract and scale bundles (*bs*) one in origin; fig. 21, transverse section of one of lowest sporophylls; ×16.

FIGS. 22–29.—*Pinus Banksiana:* figs. 22–24, from middle of cone, bundles closing up to form concentric cylinder; figs. 25–29, from lower portion of cone, phloem creeps about xylem so that concentric bundle is formed; ×34.

In all cases four bundles result (figs. 5, 12, 15, 20, 24, 29), the lower supplying the bract, the remaining three the scale.

gradually approaches a circle, and in a slightly older bud closes to form the cylinder of the shoot. The bud is united with the bract at its base, and the general appearance of a young bud and its subtending bract is suggestive of a young abietinean sporophyll.

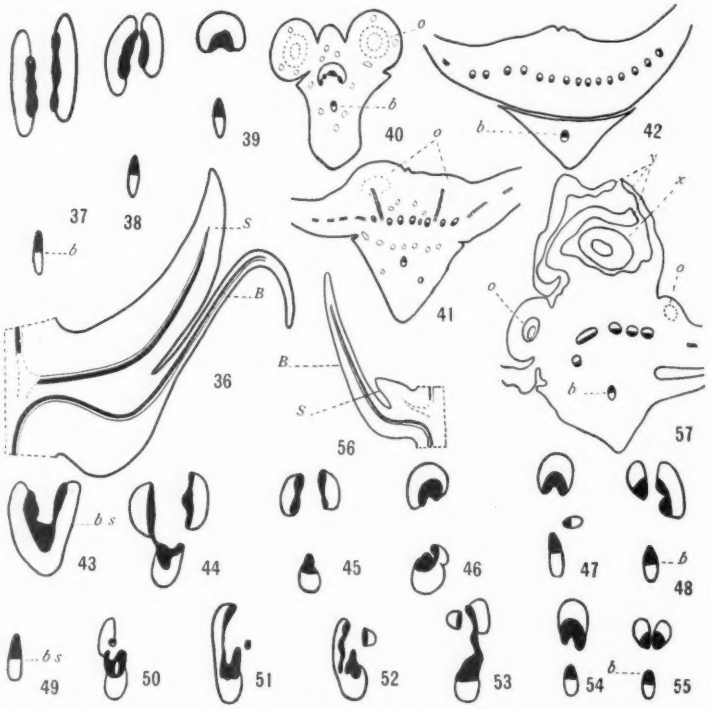
In *Keteleeria Fortunei* (figs. 36–57), one bundle originates near the base of the gap in the strobilus cylinder and supplies the bract. It remains undivided throughout its course. Two bundles, one



FIGS. 30–35.—*Pinus Banksiana*, vegetative bud: fig. 30, radial longitudinal section of lower portion of young vegetative branch; a vegetative bud in axil of each bract except at base of branch; fig. 31, origin of bract (*b*) and bud bundles; figs. 32–35, transverse sections, young bundles of bud beginning to form cylinder of branch; ×16.

from each side of the gap, supply the scale. The two bundles soon unite, forming one inverted bundle, that is, its xylem faces the xylem of the bract. The inverted bundle then breaks, forming a semicircle of bundles which spread and divide, forming in the scale a row of sixteen or more bundles. Near the ovular insertion a small concentric branch is given off to each of the two inverted ovules.

In the lower sporophylls the bract and scale bundles originate in close proximity at the base of the gap. In the lowest sporophylls the vascular supplies to both organs originate as one bundle, and



FIGS. 36–57.—*Keteleeria Fortunei:* fig. 36, longitudinal section of sporophyll, ×16; figs. 37–42, transverse sections of sporophyll from upper half of strobilus; figs. 36–39, two scale bundles divide actively, a single strand is given off to each ovule (fig. 41, *o*), ×7; figs. 43–48, from one of lower sporophylls, bract and scale bundles, close together in origin (fig. 47), gradually separate, ×34; figs. 49–55, from one of lowest sporophylls, bract and scale bundles united in origin gradually become distinct, ×34; fig. 56, longitudinal section of young sporophyll, scale (*S*) still comparatively small, ×7; fig. 57, transverse section of one of lowest sporophylls showing outgrowths (*x*, *y*) between ovules (*o*), ×16.

the two systems separate later for their respective organs. In some of the lowest sporophylls the scale supply begins blindly in the scale.

Between the ovules of the lower sporophylls is found an outgrowth which suggests an ovule with a poorly developed nucellus. At each side of and behind this median outgrowth are others which are more bractlike. In some of these xylem cells are present. Whether these abnormal excrescences mean reversions to ancestral features may be difficult to determine. The young strobilus shows no such outgrowths.

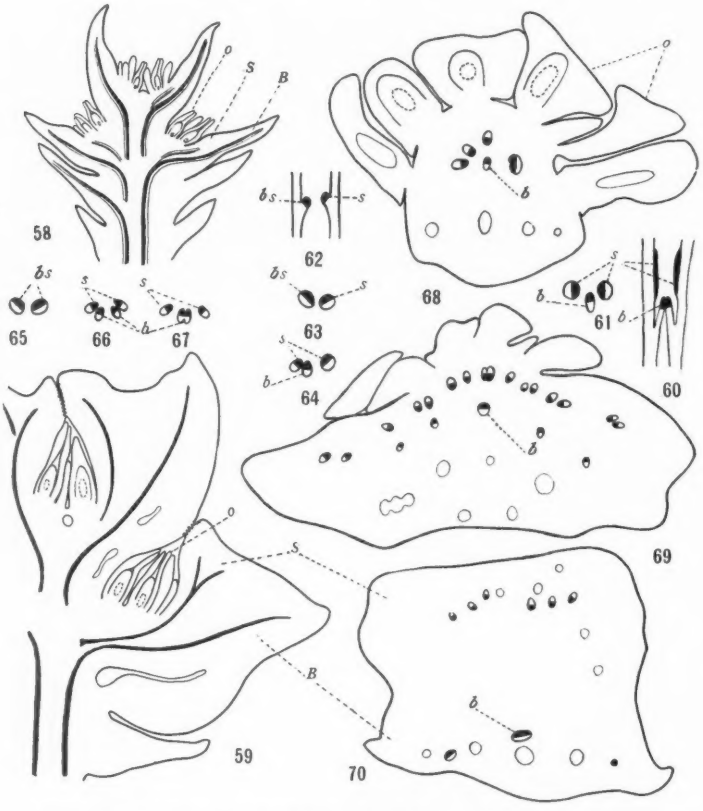
Cupressineae

The general features of the ovulate strobilus in the Cupressineae are the great reduction in the number of the sporophylls, the cyclic arrangement of the sporophylls, complete coalescence of bract and scale, and erect ovules variable in number.

The strobilus of *Cupressus Benthamii* (figs. 58–70) is composed of four decussate pairs of sporophylls. Many erect ovules are packed at the base of each sporophyll. At the megaspore mother cell stage the only evidence of the scale is a slight elevation back of the ovules and the differentiation of the scale supply near the strobilus cylinder. In somewhat later stages the free part of the scale projects outward almost as prominently as that of the bract. Contact and interlocking of epidermal cells takes place between neighboring sporophylls in such a way that the ovules become entirely inclosed.

The vascular anatomy is slightly variable in the individual sporophylls of a strobilus. As in other cyclic forms, the cylinder gap fails to close after the departure of the appendage vascular supply, and hence is continuous with the one above and below. The bract supply may arise as a single strand at one side of the continuous gap, or as two, one from each side of the gap, in which latter case the two unite into one. The scale supply originates as two bundles, one from each side some distance above the bract supply. In other cases two bundles, one from each side of the gap, compose both bract and scale supply. A strand may be given off from one of the bundles to form the bract bundle, or a strand may be given off from each bundle and the two strands unite to form the bract bundle. Whatever may be the origin, the bract bundle remains undivided to the tip of the bract. The scale bundles divide

actively; the majority come to lie near the dorsal side of the sporophyll and have inverted orientation of xylem and phloem, but several twist around to each side of the bract bundle and have

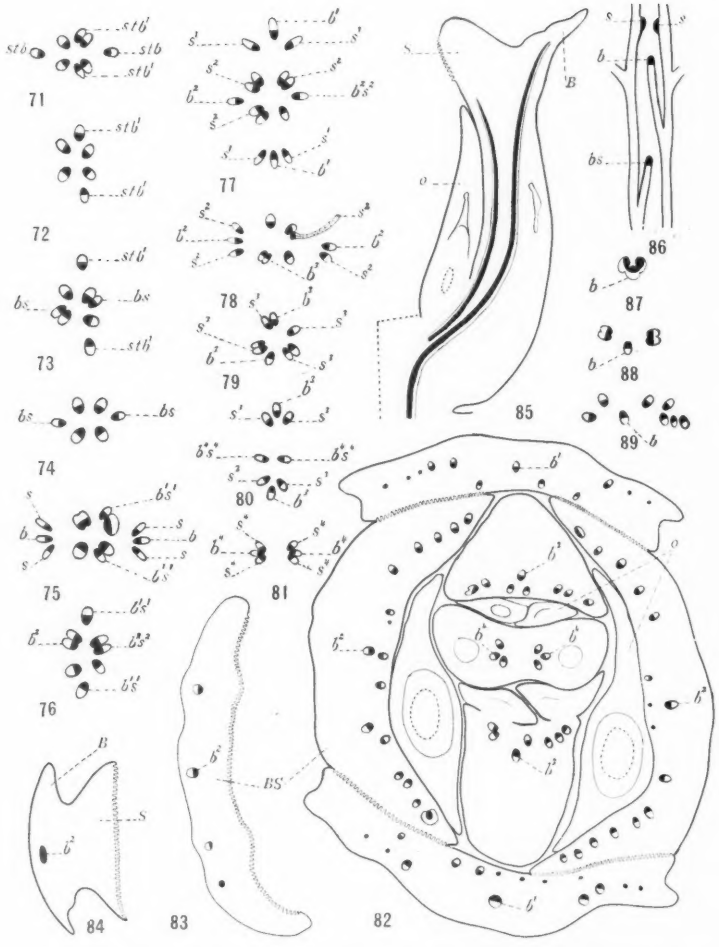


FIGS. 58–70.—*Cupressus Benthamii:* fig. 58, longitudinal section of young strobilus, scale (*S*) evident only by slight elevations on upper side of sporophyll, and beginning of scale bundles; fig. 59, longitudinal section of older strobilus, scale (*S*) evident but incorporated with tissues of bract (*B*), ×7; figs. 60–67, three methods of origin of sporophyll bundles; figs. 60, 61, bract (*b*) and scale bundles (*s*) distinct in cylinder gap; figs. 62–64, bract bundle derived from one of scale bundles (*bs*); figs. 65–67, bract bundle derived from both scale bundles (*bs*); figs. 68–70, transverse sections of sporophyll, scale bundles divide vigorously, some scale bundles persist in bract portion (fig. 70, *B*), ×16; *o*, ovule.

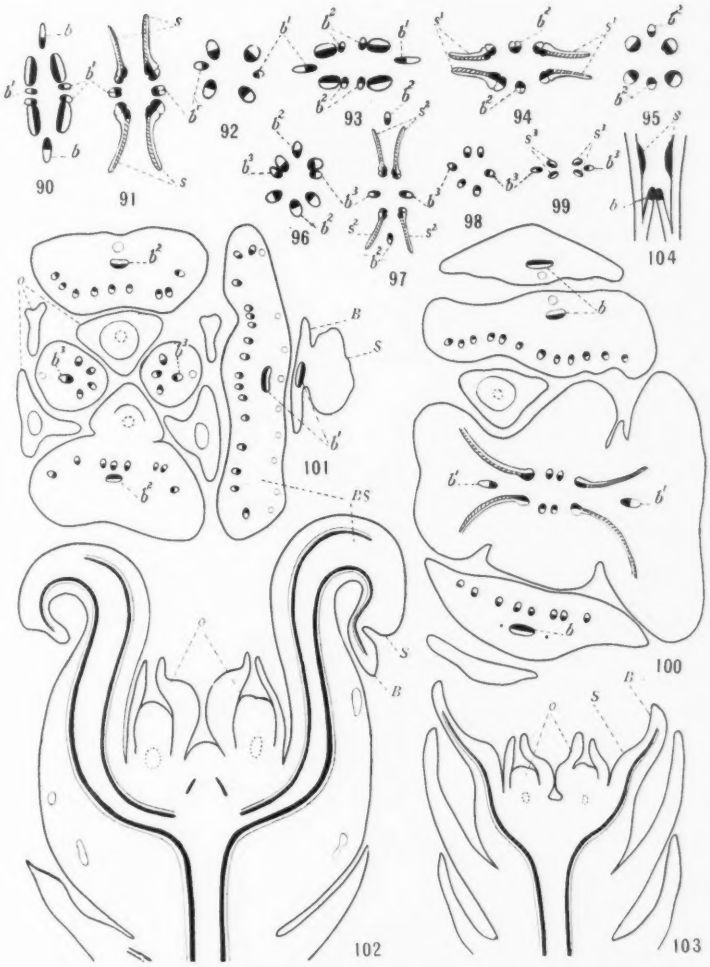
the same orientation of parts as the latter bundle. A fact to be noted in the further course of the bundles is that some of the lower scale bundles extend into the bract, though not as far as the bract bundle.

The ovulate strobilus of *Thuja occidentalis* (figs. 71–89) consists of about five decussate pairs of sporophylls. The two lower pairs are sterile, the third may have only one ovule to each sporophyll, the fourth two ovules to the sporophyll, and the fifth is sterile. The tissues of the bract and scale are so closely welded that it is impossible to distinguish one from the other except at the very tip. In the upper fertile pair of sporophylls the vascular supplies to bract and scale are distinct in origin. The supply of the first arises as one bundle at one side of the continuous gap; that of the latter as two bundles, one at each side and at a higher level. The bract bundle does not divide; the scale bundles give rise to numerous bundles, a few of which become inverted and lie near the dorsal side of the sporophyll; the majority, together with the bract bundle, form an irregular lower row of inverted bundles. In the two sterile pairs at the base, the bract and scale supply have their beginning as one bundle at one side of the long gap. This bundle soon drops into three, the median one supplying the bract, the two lateral the scale. The further course is as described before for the upper fertile sporophyll. In the lower fertile sporophyll is found a combination of the two methods of bundle origin mentioned. One of the scale bundles rises separately, but the other is combined with the bract bundle and rises at a lower level; it later separates from the bract bundle. The sterile tip pair of sporophylls receives the last two bundles of the strobilus axis. One bundle goes to each sporophyll, and drops into three bundles which divide further.

The strobilus of *Chamaecyparis Lawsoniana* (figs. 90–104) consists of about four pairs of sporophylls. In the cone represented in cross-section (figs. 100, 101), one of the lowest sporophylls has one lateral ovule, each of the sporophylls of the second pair two lateral ovules, and each of the third pair one median ovule; the fourth pair is sterile. In the early free-nuclear stage the scale is apparent only as a slight elevation on the dorsal side of the bract, which at this stage is almost straight. At a little later stage



FIGS. 71–89.—*Thuja occidentalis:* figs. 71–81, transverse section of strobilus axis, showing origin of sterile bract bundles (*stb*, *stb*^{1}) below cone, bract bundles (*b*-*b*^{4}) of sporophylls, and scale bundles (*s*-*s*^{4}); fig. 82, transverse section of same strobilus, many of scale bundles become oriented like bract bundle, two pairs of sporophylls fertile, one pair bearing one ovule per sporophyll, the other two ovules; figs. 83, 84, transverse sections near tip of sporophyll, bract (*B*) and scale (*S*) beginning to separate; fig. 85, longitudinal section of sporophyll, bract (*B*) and scale (*S*) closely united; figs. 86–89, sections parallel to cone axis; fig. 86, bract (*b*) and scale (*s*) bundles distinct in origin in upper part of strobilus, united in lower (*bs*); figs. 87–89, bract bundle separating from scale bundles; ×16.



FIGS. 90–104.—*Chamaecyparis Lawsoniana:* figs. 90–99, transverse sections of strobilus axis, showing origin of bract (b–b^3) and scale (s–s^3) bundles; figs. 100, 101, transverse sections of same strobilus, scale bundles remain close to dorsal side; one of sporophylls of lowest pair bears one lateral ovule, each of second pair two lateral ovules, each of third one median ovule, fourth pair sterile; fig. 102, longitudinal section of strobilus, bract (B) and scale (S) separate only at recurved tip of sporophyll; fig. 103, longitudinal section of younger strobilus, scale (S) evident as slight elevation on dorsal side; fig. 104, origin of bract (b) and scale bundles (s) in cylinder gap; ×16.

the growth on the dorsal side of the sporophyll is very marked, resulting in the deflexing of the coalesced bract and scale. The bract is free only at the tip of the deflexed portion. The vascular systems to the bract and scale are distinct from the strobilus cylinder. The bract bundle remains single to the tip of the bract. The two scale bundles end in a dorsal row of numerous inverted bundles. The flank bundle may turn partly and lie nearer the ventral side of the appendage.

The strobilus of *Juniperus communis* (figs. 105–113) consists of a whorl of three sporophylls united at the base and surrounding three ovules. In the older stage the sporophylls coalesce also at the tip, forming a fleshy berry-like body. The coalescence of bract and scale is complete.

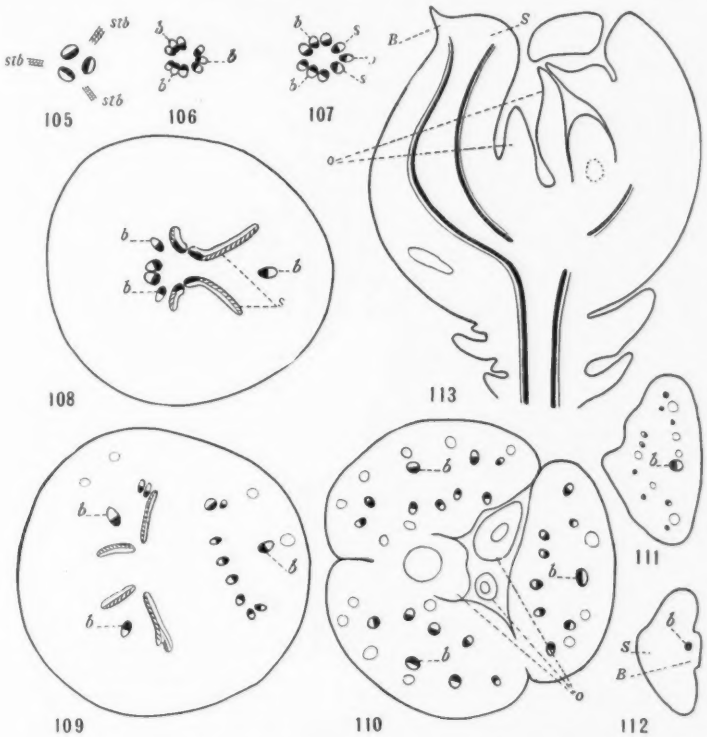
After the traces to the three bracts beneath the sporophylls have left the cylinder, each of the three remaining bundles divides into three; the median or bract bundle proceeds undivided into the bract; the two lateral or scale bundles divide, giving off some bundles to the dorsal side of sporophyll and some to ventral in such way that, including bract bundle, an oval ring of bundles with xylem facing is formed.

TAXODINEAE

The general features of the ovulate strobilus in the Taxodineae are spiral arrangement of sporophylls, reduction in number of sporophylls in some forms, considerable coalescence of bract and scale, and varying number and orientation of ovules.

In *Cryptomeria japonica* (figs. 114–128) the axis of the young strobilus is very short and the sporophylls are crowded at the broadened summit. The ovules at this stage appear to be inserted on the strobilus axis. The scale begins its development as four to six lobes between the ovules and the dorsal side of the bract. In an older stage the axis has elongated, forming a globose cone. The erect ovules, usually three in number, are definitely inserted on the sporophyll. The lobed scale is united for two-thirds of its length to the bract. In the upper portion of the cone three bundles leave the axis for the sporophyll; one at the base of the gap to supply the bract, and one from each side of gap to supply the scale.

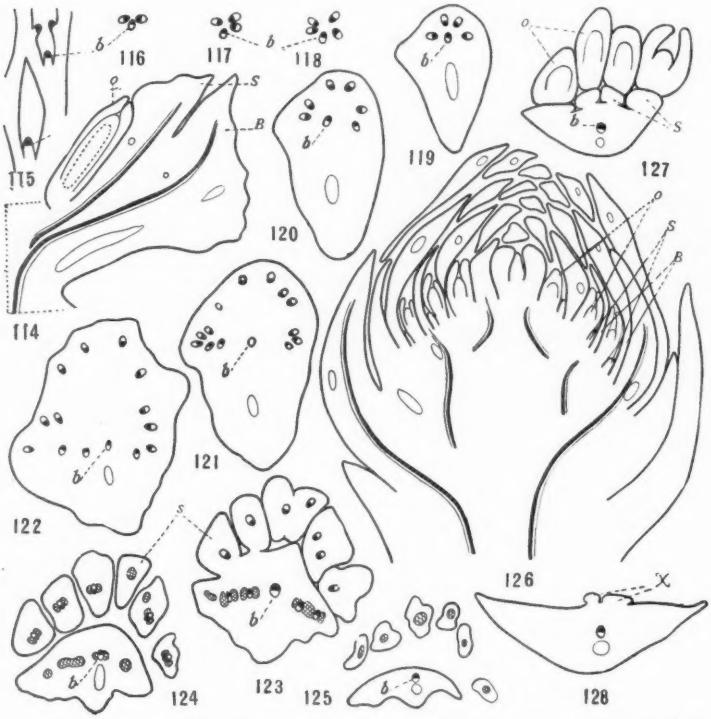
The two scale bundles divide, resulting in the sporophyll in a ring of bundles with xylem facing inward. Included in the lower portion of the ring is the bract bundle. One and sometimes two bundles enter each lobe of the scale. A number of the scale bundles



FIGS. 105–113.—*Juniperus communis:* figs. 105–110, course of bundles from base of strobilus to middle of three sporophylls; sporophylls closely coalesced at base; some of scale bundles come to lie in same plane as bract bundle (*b*); figs. 111, 112, transverse sections of tip of sporophyll, bract apparent as small ridge (*B*); fig. 113, longitudinal section of strobilus; *o*, ovule; *stb*, sterile bracts below strobilus; ×16.

pass into the free portion of the bract at each side of the bract bundle and have the same orientation of parts as the bract bundle. The ending of each bundle is accompanied by short irregular tracheids. The scale bundle may arise in closer proximity to the

bract bundle; in the lower sporophylls scale and bract supplies spring from the base of the gap as one large bundle which breaks into three; these latter supply the sporophyll parts as described before.



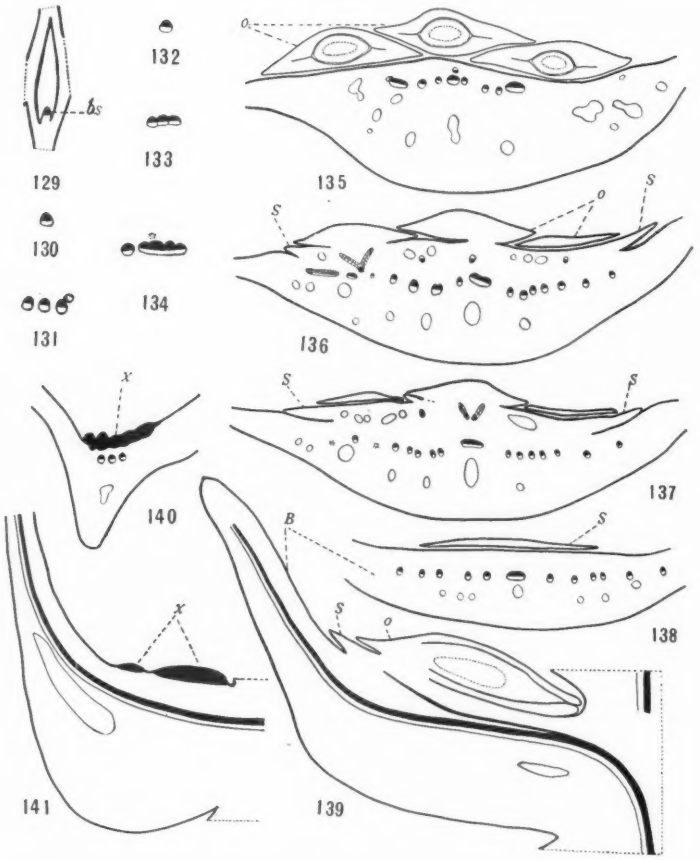
FIGS. 114–128.—*Cryptomeria japonica:* fig. 114, longitudinal section of sporophyll; fig. 115, origin of bract (*b*) and scale bundles in upper part of strobilus distinct, in lower part united (*bs*); figs. 116–125, transverse sections, further course of bundles in sporophyll; bract bundle (*b*) remains undivided, some of scale bundles come to lie in same plane as bract bundle (figs. 121, 122); lobes of scale separate from one another and from bract, each lobe receiving usually one bundle; remaining scale bundles enter free portion of bract (figs. 123, 124); bundles end in large irregular tracheids; ovules not represented; ×7; fig. 126, longitudinal section of young strobilus, scale (*S*) appears as small lobes between bract (*B*) and ovules (*o*), ×16; fig. 127, transverse section of young sporophyll, showing bract (*B*), four lobes of scale (*S*), and ovules (*o*); fig. 128, transverse section of one of uppermost sterile sporophylls, showing outgrowths similar to lobes of scale in fig. 127, ×34.

The strobilus of *Taxodium distichum* possesses the same general characters as described for *Cryptomeria japonica*.

The strobilus of *Cunninghamia Davidiana* (figs. 129–141) is composed of a relatively large number of sporophylls. The scale is united to the bract, with the exception of a small edge distal to the insertion of the three inverted and slightly winged ovules. The vascular supply to the sporophyll departs from the cylinder gap as one large bundle; this bundle soon divides more or less definitely into three; a further division takes place until a row of fifteen or more normally oriented bundles results in the expanded part of the sporophyll. In the earlier course of the branching of the bundles weak strands separate from the lateral bundles and swing around 180° so as to lie on the dorsal side of sporophyll; some of these strands fork, so that an upper row of five or six inverted bundles results; some of these bundles may begin blindly; near the insertion of the ovules one or two strands bend toward the chalaza and end there or a short distance behind the chalaza. Owing to the fact that the bundles in the lower row adhere more or less in the earlier course of division, it is difficult to determine whether the median of the three first bundles passes undivided into the narrow portion of the bract. It is accompanied, however, by branches from the lateral bundles for some distance into the free portion of the bract. At the tip and base of the strobilus are sterile sporophylls. These have a vascular anatomy similar to that of the fertile sporophylls, with the exception of the absence of the upper inverted bundles in the former. Neither scale nor ovules are present, but in place of these appear slight excrescences with different staining reactions.

Araucarineae

The ovulate strobilus in the Araucarineae is composed of numerous spirally arranged and closely compacted sporophylls. Each sporophyll bears one inverted ovule, which is imbedded in the sporophyll tissues in *Araucaria*, and naked and winged on one side in *Agathis*. Another feature of the Araucarineae of significance in this connection is the branching of the sporophyll bundle in the



FIGS. 129–141.—*Cunninghamia Davidiana:* fig. 129, vascular supplies to bract and scale leave cylinder gap as one bundle (*bs*); figs. 130, 131, and 132–134, splitting up of single bundle; figs. 135–138, transverse sections of sporophyll small strands split off from lower series or begin blindly (fig. 134, dots) and come to lie on dorsal side of sporophyll; the majority of these small bundles finally bend toward chalaza of ovules and end there; the majority of lower bundles enter free portion of bract (fig. 138, *B*) beyond insertion of scale (*S*); fig. 139, longitudinal section of sporophyll, scale (*S*) appears as flap beyond insertion of ovules (*o*); fig. 140, transverse section of sterile sporophyll near tip of strobilus, dark stained elevations (*x*) taking place of scale and ovules; fig. 141, longitudinal section of sterile sporophyll at base of cone, similar outgrowths (*x*) as in fig. 140; ×7.

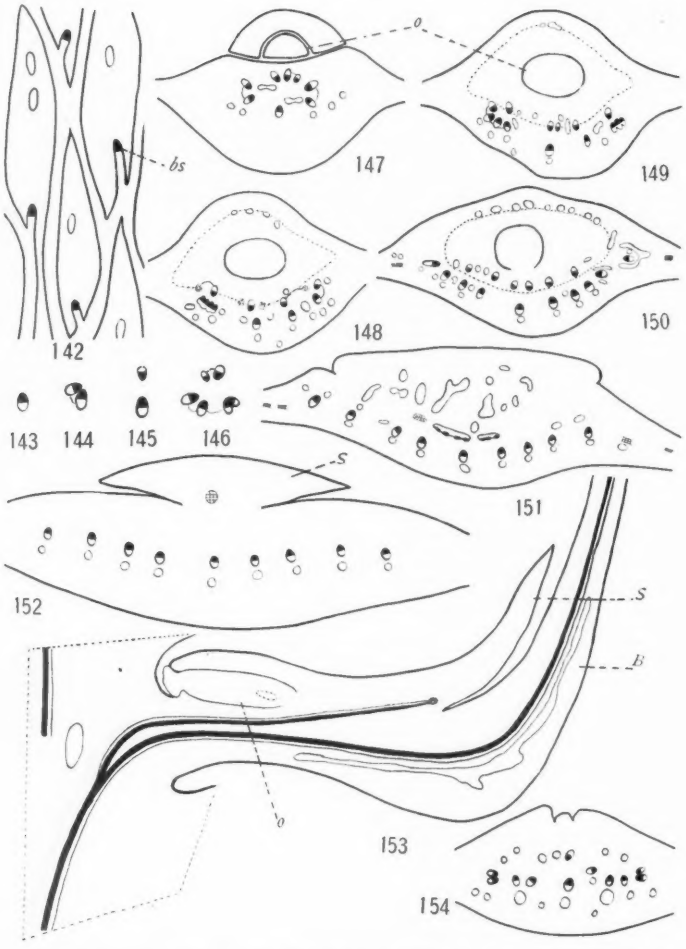
vegetative leaf. This is a characteristic which so far as investigated occurs outside the Araucarineae only in *Podocarpus Nageia*.

The sporophyll of *Araucaria* is characterized by the so-called ligule, which there is good reason to believe is homologous with the scale described in the foregoing groups. In the young strobilus of *Araucaria Rulei* and *Araucaria Balansi* the comparatively small ligule is attached to the bract at its base only, the greater portion being free. In the older strobilus it is free only at the tip. Distal to the line of coalescence of bract and scale the bract remains thick and wide, then becomes narrow and stiff, resembling the bracts at the base of the strobilus.

The vascular supply to the sporophyll of *A. Balansi* (figs. 142–154) arises as a single bundle near the base of the gap in the strobilus cylinder. In the middle of the cortex the single bundle divides into two unequal parts, the smaller of which twists through an angle of 180° so as to lie above the parent bundle with its xylem facing the xylem of the latter. The upper bundle may or may not divide at this stage; the lower bundle divides into two or three; in case of two, one bundle soon divides and a median lower bundle is formed. The lateral bundles divide actively; some of the resulting bundles become inverted and lie on a level with the upper bundle, others normally oriented come to lie on a level with the lower median bundle. Where the sporophyll broadens, branches with normal orientation enter the wings. Behind the ovules the bundles of the upper series begin to converge in groups, and finally end in masses of irregular tracheids. A bundle is sometimes found to continue almost to the free portion of the ligule. Where the bract becomes narrow, the lower bundles also end, with the exception of about three median ones which extend into the slender portion. In the lowest sporophylls, where the ovule and scale are poorly developed or absent, the upper bundles are weak and few in number, or wanting.

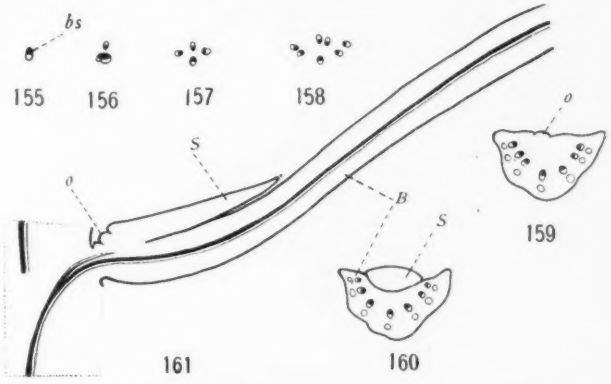
In the other forms investigated, *A. Rulei* (figs. 155–161) and *A. excelsa*, the general features are as in the above-described species.

The strobilus of *Agathis australis* (figs. 162–170) is composed of numerous sporophylls which are very closely packed, probably owing to the shortening of the strobilus axis. A ligule, as found in



FIGS. 142–154.—*Araucaria Balansi:* fig. 142, vascular supply to sporophyll springs from single strand near base of cylinder gap; figs. 143–146, course of bundles in cortex; figs. 147–152, transverse sections of sporophyll, lines drawn between bundles indicate last division; upper bundles run together in groups and end in large irregular tracheids (fig. 151); one persists almost to free portion of scale (fig. 152); fig. 153, longitudinal section of sporophyll (*S*, scale or ligule; *B*, bract, *o*, ovule); fig. 154, transverse section of sterile sporophyll at base of strobilus, upper bundles few; ×8.5.

Araucaria, is absent, but the general appearance of a slight elevation behind the ovule suggests the possibility of a fused body. The vascular supply begins as a single stout trace a little to one side at the base of the short wide cylinder gap. The trace increases in size, and in the outer one-third of the cortex a branching begins which in the lamina of the scale results in about thirteen bundles. About half-way between the insertion of the sporophyll and the insertion of the ovule a small strand splits off from one of the median bundles, swings around 180°, and becomes an inverted bundle

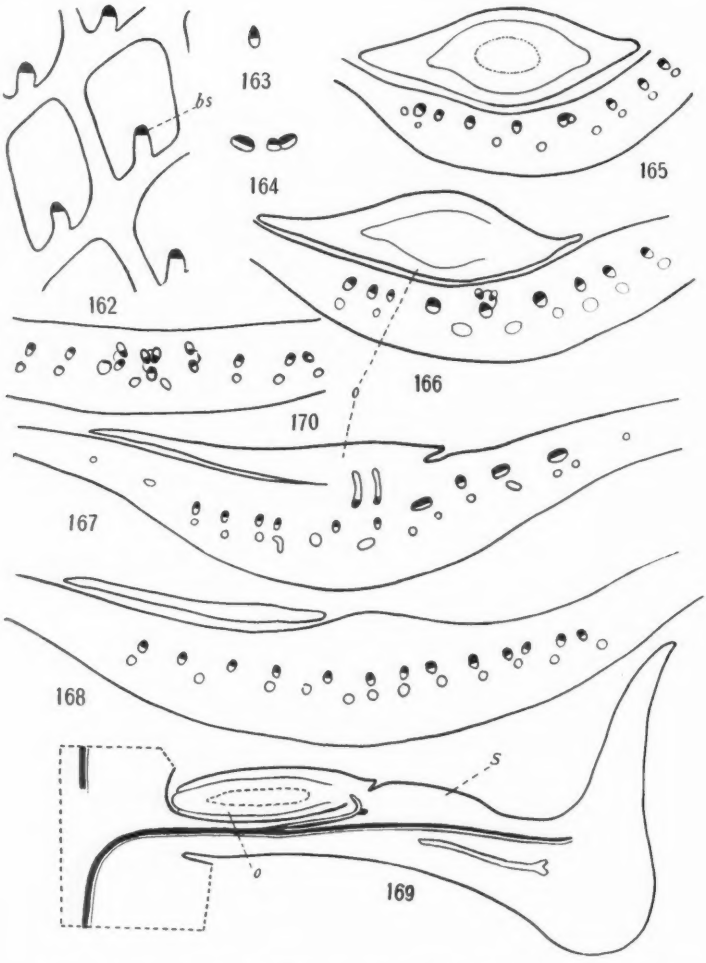


FIGS. 155–161.—*Araucaria Rulei*, young sporophyll: figs. 155–160, course of bundles from strobilus axis to free portion of bract, upper bundles differentiated in cortex and base of sporophyll (*B*, bract; *S*, scale; *o*, ovule); fig. 161, longitudinal section of sporophyll; ×8.5.

opposite its sister bundle. The inverted strand may fork, and also inverted strands may spring from several of the median lower bundles and these strands may divide so that the number of upper bundles varies from one to several. In any case, each of the upper bundles, after giving off a phloem-like strand to each ovule, ends in large irregular tracheids.

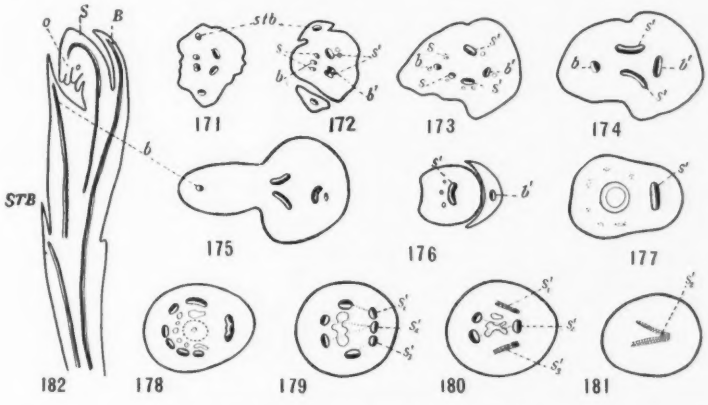
PODOCARPINEAE

In most of the Podocarpineae a definite strobilus is absent, the fructification consisting in most cases of one or two fertile sporophylls. In many forms there is a tendency for some part of the fructification to mature fleshy.



FIGS. 162–170.—*Agathis australis:* fig. 162, vascular supply to sporophyll springs from single strand near base of cylinder gap; figs. 163–168, course of bundles in cortex and sporophyll, a bundle springs from a median bundle, becomes inverted (fig. 166), then breaks into two branches which enter chalaza of ovule (fig. 168), ×8.5; fig. 169, longitudinal section of sporophyll, an elevation appears distal to insertion of ovule; fig. 170, transverse section of sporophyll, inverted bundles have sprung from three of median lower.

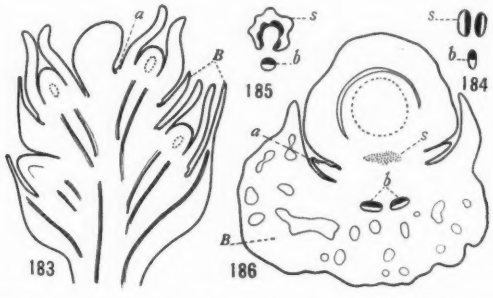
In a species of the subgenus *Eupodocarpus* (figs. 171–182) the ovule-bearing branch is a dwarf lateral branch bearing at its tip one and occasionally two fertile sporophylls, and a few small bracts some distance below. The single inverted ovule is imbedded in the tissues of the "epimatium," which there is evidence for believing to be homologous with the ovuliferous scale in other conifers. At maturity the portion of the fruiting branch between the fertile sporophylls and the upper sterile bracts becomes fleshy.



FIGS. 171–182.—*Podocarpus* (sp. of *Eupodocarpus*): figs. 171–181, transverse sections from base of uppermost sterile bracts (fig. 182, *STB*) to tip of strobilus; *stb*, bundles supplying sterile pair of bracts; *b*, bundle supplying sterile bract opposite fertile sporophyll; *s*, bundles inclining toward sterile bract then ending; b^1, bundle supplying bract of fertile sporophyll; s^1, two bundles uniting into one enter scale of fertile sporophyll where the single bundle breaks into three (fig. 179, s^1_1, s^1_2, s^1_3); distal to chalaza each of three bundles bends to pass down dorsal side of ovule (figs. 180, 181; fig. 179; dotted lines between bundles indicate that one bundle is a continuation of the other); fig. 182, longitudinal section of strobilus; ×7.

The vascular anatomy was investigated only in cases of one fertile sporophyll. The vascular supply of the branch axis, after the traces to the sterile bracts have gone out, consists of three small and three large bundles. The median of the three smaller bundles enters what in the young stages appears like a bract opposite the fertile sporophyll; the two small lateral bundles bend in the same direction as the small median bundle, then end. The

median of the three larger bundles supplies the bract of the fertile sporophyll; each of the lateral bundles twists so as to lie with xylem facing the bract bundle, then the two unite into one bundle which proceeds into the scale. The single bundle increases in size, and on nearing the chalaza of the ovule breaks into three; at the base of the ovule each of the lateral branches curves over and passes downward in the tissues of the scale flanking the ovule. The median bundle proceeds slightly farther, then curves over the base of the ovule, and at the same time breaks into two branches which pass downward in the portion of the scale on the dorsal side of the ovule. The recurved branches of the scale supply fork so that



FIGS. 183–186.—*Phyllocladus alpinus:* fig. 183, longitudinal section of young strobilus, aril (*a*) appearing around the base of the ovule; figs. 184, 185, scale (*s*) bundles unite to form a semicircle; fig. 186, transverse section of an older sporophyll, bract bundle (*b*) forks in this instance, scale bundle (*s*) ends at base of ovule; ×61.

in cross-section a ring of bundles with xylem facing outward surrounds the ovule.

In another species of *Podocarpus* investigated the scale bundle divides into two instead of three branches. Each of these two curves at the chalazal end of the ovule and passes downward, one at each side of the ovule. The crests of the two curves are connected by irregular xylem cells, and a strand of similar tissue extends from each crest outward into the protuberance on the scale behind the ovule.

Phyllocladus alpinus (figs. 183–186) consists of a globose strobilus of few sporophylls. The ovule is sessile in the axil of the bract. The vascular supply to the bract springs from the base

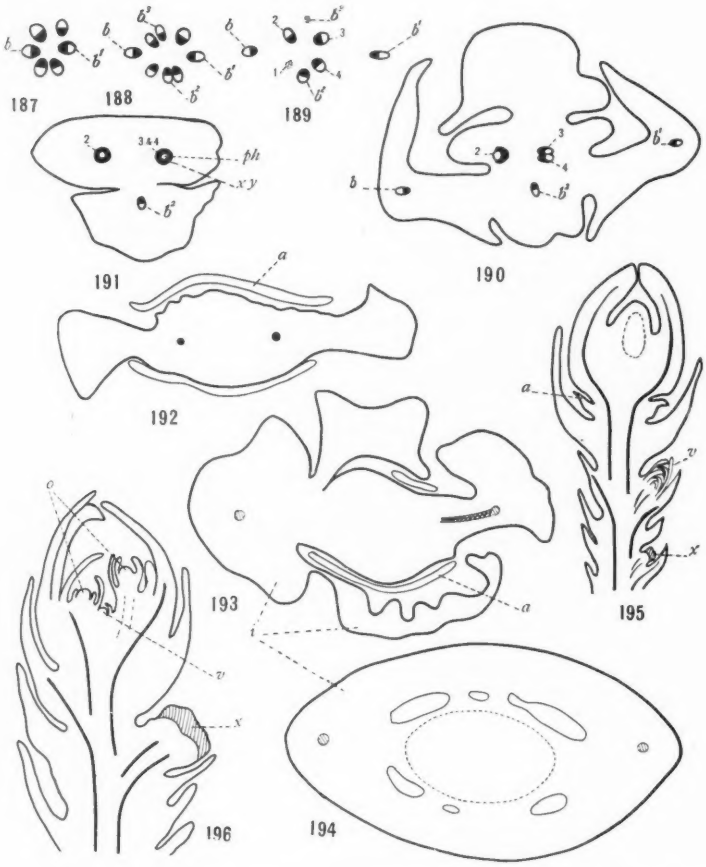
of the gap. Two bundles from the sides of the gap unite to form a semicircle which ends at the base of the ovule.

Taxineae

Perhaps the most outstanding features of the Taxineae in this connection are the distinctly terminal ovule in some forms and the development of the aril in the later stages.

In *Taxus baccata* (figs. 187–196) the bud of the primary fertile and dwarf branch develops in the axil of a leaf of a long branch of the first season's growth; the second season the ovule matures. Near the tip of the primary fertile and dwarf branch is a secondary dwarf branch bearing a few decussate pairs of bracts and terminally an ovule. Occasionally two secondary dwarf ovule-bearing branches are produced, one at each side of the terminal vegetative bud of the primary branch. Beneath the ovuliferous branch or branches the primary shoot is covered with scalelike bracts. The growth of the terminal vegetative bud of the primary shoot is usually arrested by the active development of the secondary ovuliferous branch, so that the latter appears to be terminal. Ovules are found maturing on the second, third, and fourth seasons' growth, instead of on the second season's only. This implies that the ovule in some cases fails to mature the second season, or that the vegetative bud of the primary dwarf branch may resume activity and produce other ovuliferous branches; the latter seems most probable; also the presence of branch scars on the older and more elongated dwarf shoots suggests that the latter conclusion may be drawn.

After the bundles to the upper sterile bracts have either passed into their respective appendages or have ended before entering the latter, the vascular supply of the axis of the ovule-producing branch consists of four bundles. These bundles unite in pairs, one bundle from each side of the bract bundle of the next lower pair, and not one from each side of the bract of the last pair as is usually the case where the united bundle is to supply some axillary structure. The xylem creeps around the phloem in each of the two bundles formed. Sometimes one of the four bundles in the axis ends, whereupon the odd bundle behaves like the fused bundle



FIGS. 187–196.—*Taxus baccata:* figs. 187–194, transverse sections upper part of fertile branch to middle or ovule; b, b^1, bundles to supply pair of bracts; b^2, b^3, bundles to supply uppermost pair of bracts; b^3 ends before entering bract; 1, ends in axis; 2, xylem surrounds phloem; 3, 4, unite into one bundle, xylem surrounds phloem (fig. 191), the two bundles continue as weak strands of xylem cells in base of each wing of ovule, xylem cells are soon replaced by elongated slightly thickened cells without true xylem markings, ×16; fig. 195, longitudinal section of fertile branch, terminal vegetative bud (v) is turned aside by rapidly growing ovule bearing branch; x, scar left by vegetative or fertile bud or branch, ×7; fig. 196, young fertile branch showing two lateral ovule-bearing branches and a terminal vegetative bud (v); x, scar as in fig. 195, ×16.

(figs. 183, 186). At the base of the ovule each bundle passes into a mass of short irregular tracheids of large caliber. From each mass arises a small strand consisting of poorly developed xylem soon replaced by elongated thickened cells without xylem markings. Each strand passes upward in the thickened ridge of the ovule.

Discussion

Assuming that the megasporophyll in all the forms is a composite organ, consisting of bract and axillary scale, the investigated forms may be divided into four general groups based on the relation of bract and scale to one another.

In the first group the bract and scale are separate almost to the base of the appendage and both are about equally prominent. Here belong *Keteleeria* (fig. 36), *Pseudotsuga*, species of *Abies*, and species of *Larix*.

In the second group the bract and scale are separate as in the first group, but the bract, at least in the later stages, is much less prominent than the scale, and in certain instances appears distinctly to be on its way to obliteration. In this group belong species of *Abies* (**2**), species of *Larix*, *Tsuga*, *Picea*, *Pinus* (figs. 1, 2), and species of *Podocarpus* and *Dacrydium* (**4**); *Cedrus Libani* (**2**) and the lower sporophylls of *Pinus Banksiana* (fig. 2) show the bract in process of extinction. In species of *Podocarpus* the scale has folded toward its dorsal side, thus forming the second integument or epimatium of the inverted ovule (fig. 182).

In the third group the bract and scale are considerably to completely welded, but the fused structure shows some evidence of its double nature. Within this group are *Sciadopitys* (**2**), *Sequoia* (**2**), *Cunninghamia* (fig. 139), species of *Arthrotaxis* (**1**), *Cryptomeria* (fig. 114), *Taxodium*, *Thuja* (fig. 85), *Cupressus* (fig. 59), *Chamaecyparis* (fig. 102), *Juniperus* (fig. 113), *Araucaria* (fig. 153), and *Podocarpus dacrydioides* (**4**). In young strobili of *Araucaria Rulei* (fig. 161) and *Cryptomeria japonica* (fig. 126) the bract and scale are distinct almost to the base, and the fused portion becomes comparatively large in the subsequent development of the organ. In *Cupressus Benthamii* (fig. 58), *Thuja occidentalis*, *Chamaecyparis Lawsoniana* (fig. 103), and *Juniperus communis* the scale in the

young strobilus is one with the bract and becomes evident in the later stages by the comparatively rapid growth of the tissues on the dorsal side of the composite organ.

In the fourth group there is no external evidence of more than one organ. Into this group fall *Arthrotaxis selaginoides* (**1**), *Agathis* (fig. 169), *Saxegothaea* (**5, 8**), *Phyllocladus* (fig. 183), *Taxus* (fig. 191), *Torreya* (**6, 7**), and *Cephalotaxus* (**6, 7**). It should not be surprising to find forms in which the welding has taken place beyond the recognition of more than a single structure when one considers to what extent this process has taken place in *Chamaecyparis*, *Juniperus*, *Thuja*, *Cunninghamia*, and *Podocarpus dacrydioides* (**4**). The low cushion behind the ovule in *Agathis australis* suggests the complete fusion of a scale to a large bract; a similar fusion is nearing its completion in *Cunninghamia Davidiana*.

On the basis of vascular anatomy the investigated sporophylls fall into two general groups.

In the first group the bract and scale supply arises as separate bundles in the cylinder gap. In this group belong in general those forms in which the two sporophyll parts are separate and fairly well developed, as the seed-producing sporophylls of *Pinus Keteleeria*, *Picea*, *Larix*, *Tsuga*, *Pseudotsuga*, and *Abies* (**2**). To this group belong also many in which the two sporophyll members present considerable to complete fusion, as *Araucaria Bidwilli* (**1, 3, 10**), *Chamaecyparis Lawsoniana*, *Juniperus communis*, and the upper sporophylls of *Thuja occidentalis*, *Cupressus Benthamii*, and *Cryptomeria japonica*. This group includes also some in which the sporophyll is evident only as a single organ, namely *Phyllocladus* and *Cephalotaxus* (**6, 7**).

In *Podocarpus* and *Dacrydium*, where the strobilus consists of one or two sporophylls, and in *Juniperus communis*, the sporophylls receive the final bundles of the axis. There is in these instances no cylinder gap, and the bract and scale supplies, at least in the forms investigated by the writer, result from the division of one of the final bundles in the axis. The early division of the bundle in the tip of the axis perhaps justifies the placing of these forms in this group.

In the second group based on vascular anatomy the bract and scale vascular supplies are more or less intimately united into one bundle which springs from the base of the cylinder gap.

Of sporophylls with parts separate there belong here the lower sporophylls of *Pinus Banksiana*, *P. maritima*, and *Keteleeria Fortunei* (the ovules in these sporophylls are to greater or less extent abortive), and *Cedrus Libani* (**2**). Of the sporophylls with parts considerably united there fall into this group those of *Cunninghamia*, *Arthrotaxis laxifolia* (**1**), most species of *Araucaria* (**1, 3, 6, 7, 9, 10**), and the lower sporophylls of *Cryptomeria japonica*, *Cupressus Benthamii*, and *Thuja occidentalis*. Most of the apparently simple sporophylls are included in this group, as those of *Agathis*, *Saxegothaea* (**5, 8**), and *Arthrotaxis selaginoides* (**1**).

The degree of welding of the bract and scale vascular supplies varies considerably. In *Arthrotaxis selaginoides*, *Agathis*, *Araucaria*, and *Saxegothaea* the two remain united into one bundle for greater or less distance in the cortex; in most of the others the single bundle divides early; but in many cases, where the two sporophyll parts have fused extensively, branches of the scale supply swing about to lie on the ventral side of the appendage at each side of the bract bundle. This fact is well illustrated in *Thuja occidentalis*, *Juniperus communis*, *Cupressus Benthamii*, and *Cryptomeria japonica*. In *Cupressus Benthamii* and *Cryptomeria japonica* the scale bundles at either side of the bract bundle even accompany the bract bundle into the free portion of the bract.

Bundle distribution is generally directly related to the size of the organ supplied, hence the bundles extend into the most expanded region of the sporophyll, whether that particular region represents bract or scale.

In *Cunninghamia*, *Araucaria*, and *Agathis*, in which absence of sporophylls with separate bract and scale supplies makes comparison impossible, it is difficult to determine with certainty what is bract and what is scale supply. The matter is further complicated by the presence in the last two genera of a branching bundle in the vegetative leaf, a condition which probably implies a branching bract bundle in the bract of the sporophyll as well. And, further, *Cupressus Benthamii* and *Cryptomeria* have clearly shown

that the final destination of a bundle does not always determine to which sporophyll part it belongs. It is to be suspected that the bundle system of *Agathis* and *Araucaria* represents a complex of bract and scale bundles. Judging by the course of events in other conifers with single-veined vegetative leaves, it may be suggested that the large median lower bundle in *Cunninghamia Davidiana* is the bract bundle proper, which is accompanied for some distance into the free portion of the bract by a few scale bundles.

Taxus presents some features which perhaps ought to be mentioned. The single ovule is produced terminally on a secondary dwarf branch clothed with a few pairs of decussate bracts. The primary dwarf branch may occasionally become a long branch by the resumption of growth by its terminal bud. In all of the many ovules examined the ovule is flattened transversely to the uppermost pair of bracts. The four final bundles of the branch of the axis which fuse in pairs before entering the two wings of the ovule fuse in pairs across the next lower pair of bracts, and not across the uppermost pair of bracts, a behavior which is contrary to what should be expected if the fused bundle were destined to supply an axillary structure. The dying out of bundles near the tip of the axis and the consequent failure to supply the uppermost bracts or enter into the formation of the ovuliferous supplies, as the case may be, suggest that a general reduction and loss of parts is taking place. The terminal position of the ovule, the flattening of the ovule transversely to the uppermost bracts, and the fusion in pairs of the final bundles of the axis in the definite way to form the two bundles of the wings of the ovule suggest a structure which might result from a process well under way in *Juniperus communis*, namely the fusion of sporophylls to form a single structure. This in *Taxus* would imply the reduction of the ovules to one, the complete fusion of two sporophylls to the integument of the ovule, and finally the reduction of the vascular supply of each sporophyll to the single weak bundle present in the wing of the ovule. In view of the modifications that are apparently taking place in other conifers such a course of events may be possible, but further investigation is necessary.

The ovule of *Phyllocladus glauca* presents a slightly simpler situation than that of *Taxus*. The two bundles beginning from the sides of the gap and ending at the base of the ovule are probably the only vestige of the scale. The aril may be no more than an outgrowth such as appears in connection with the ripening of ovules in the podocarps. The outer integument of *Torreya* may be a more complex organ.

If any probable conclusions can be made concerning the ovulate structure of the Taxineae, they must in any event be preceded by a more thorough investigation of the different forms.

In spite of striking modifications, the origin of the megasporophyll is homologous throughout the conifers. As to the identity of the organ in question there seems nothing new to be added. The gradation from foliage leaves to bracts of sporophylls is so definite in many forms, as in *Larix* and *Pseudotsuga*, that the homology of one with the other need not be questioned. The scale is the organ in doubt. Its axillary position and the origin of the vascular supply when separate from that of the bract justifies the theory that it is some modification of a fertile branch. Through shortening of the axis and rather delayed development of the shoot in general, together with a relatively earlier development of the ovules, the semicircle of bundles at the base of an ordinary shoot failed to form the cylinder, but instead flattened out into an arc and in some cases even into a straight line.

Summary

1. In the evolution of the ovulate strobilus in members of the Coniferales, two general tendencies are apparent: (1) the reduction in number of sporophylls in the strobilus; (2) the modification of a compound sporophyll into an apparently simple sporophyll; the latter appears in diverse disguises, but in general implies loss of one of the sporophyll members or welding of the two.

2. Strobilus reduction has reached its highest expression in members of the Cupressineae, Taxineae, and Podocarpineae; one type of strobilus reduction is represented by the general sterilization and reduction of parts in the lower sporophylls of *Pinus*.

3. Simplification of a compound sporophyll has been attained to fullest extent in *Arthrotaxis selaginoides*, *Agathis*, and *Saxegothaea*, and possibly others; an extensive reduction of bract occurs in *Cedrus Libani* and the lower sporophylls of *Pinus maritima;* the scale in *Phyllocladus* is probably reduced so as to be represented only by a distinct ovular supply; the welding of the two organs is complete in *Juniperus communis* and *Chamaecyparis Lawsoniana*.

4. Fusion of bract and scale vascular supplies does not directly parallel fusion of bract and scale.

5. Separate origin of bract and scale vascular supplies occurs most generally in the Podocarpineae and Abietineae; fusion of bract and scale supplies has reached its highest expression in the Araucarineae; both types of bundle origin are represented in the same strobilus in *Cryptomeria japonica*, *Cupressus Benthamii*, and the lower sporophylls of *Pinus*.

6. The bract bundle in plants with uninerved vegetative leaves divides only slightly if at all; the extent of the scale bundle system is directly related to the size of the organ supplied.

7. The scale bundles in the Abietineae and *Chamaecyparis Lawsoniana* form in the expanded portion of the organ a straight row or arc; in members of the Taxodineae and Cupressineae scale bundles swing around so as to lie at each side of the bract bundle.

8. In *Cryptomeria japonica* and *Cupressus Benthamii* and perhaps *Cunninghamia Davidiana* scale bundles accompany the bract bundle into the free portion of the bract.

9. A branching bundle in the vegetative leaf in *Araucaria* and *Agathis* probably implies a branching bundle in the bract of the sporophyll; the vascular system in the megasporophyll is probably a complex of bract and scale bundles.

10. In species of *Podocarpus* the scale bundles continue in the portion of the scale folded toward the dorsal side, forming the epimatium of the ovule.

The author is indebted to Professor J. M. COULTER and Dr. C. J. CHAMBERLAIN for valuable suggestions, and to the latter also for excellent material.

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THE INDEX OF FOLIAR TRANSPIRING POWER AS AN INDICATOR OF PERMANENT WILTING IN PLANTS

A. L. BAKKE

(WITH ONE FIGURE)

The index of transpiring power as put forward by LIVINGSTON[1] is taken as a measure of the power of leaves to supply moisture to the surrounding air. The reciprocal of this index is a measure of the power of leaves to retain water against the drying influence of the surroundings. The index of transpiring power for any leaf as found by means of cobalt chloride paper represents the power of the leaf to give off water, this being measured in terms of the similar power possessed, at the same temperature, by a saturated blotting paper surface blanketed by a millimeter of air. The index for an entire leaf is obtained by averaging the indices obtained for the two leaf surfaces. Indices less than unity represent leaf surfaces with lower power of giving off water than is possessed by the standard evaporating surface. Those greater than unity can give off water faster than does the standard surface at the same temperature. The work of BRIGGS and SHANTZ,[2] that of CALDWELL,[3] and that of SHIVE and LIVINGSTON[4] have recently brought forth the concept of permanent wilting in plants. This is that stage of progres-

[1] LIVINGSTON, B. E., The resistance offered by leaves to transpirational water loss. Plant World **16**:1–35. 1913.

[2] BRIGGS, L. J., and SHANTZ, H. L., The wilting coefficient and its indirect determination. BOT. GAZ. **53**:20–37. 1912.

———, The relative wilting coefficient for different plants. BOT. GAZ. **53**:229–235. 1912.

———, The wilting coefficient for different plants and its indirect determination. U.S. Dept. Agric., Bur. Pl. Ind. Bull. 230. 1912.

[3] CALDWELL, J. S., The relation of environmental conditions to the phenomenon of permanent wilting in plants. Physiol. Res. **1**:1–56. 1913.

[4] SHIVE, J. W., and LIVINGSTON, B. E., The relation of atmospheric evaporating power to soil moisture content at permanent wilting in plants. Plant World **17**: 81–121. 1914.

sive wilting at which the plant cannot recover turgidity if inclosed for 24 hours (without watering of the soil) in a chamber of saturated air. Interest in this stage of wilting centers mainly about the determination of the residual moisture content of the soil at the time when permanent wilting is attained. It is unnecessary here to review the important contributions already made in this connection, but it may be safely stated that the concept of permanent wilting promises to be of great importance in soil moisture studies for ecological and agricultural interpretation. Besides the authors above mentioned, ALWAY[5] has studied the relation of plants to soil moisture, with results bearing upon this general question.

It is somewhat difficult to determine just when the stage of permanent wilting is attained; an observer can never be quite sure whether a plant is permanently wilted or not until after the 24-hour exposure in the moist chamber, and there is always considerable danger that the wilting may be carried too far. This difficulty suggested to the writer the possibility of employing the cobalt chloride paper test of foliar transpiration power as an indicator of attainment of permanent wilting.

In the summer of 1913, at the Desert Laboratory of the Carnegie Institution, some preliminary studies were carried out upon the relation of the index of foliar transpiring power to the stage of wilting in plants. It was the writer's privilege to carry out these tests upon plants actually employed in the work of SHIVE and LIVINGSTON, then in progress. The results of some of these tests have already been published.[6] They clearly indicate a direct relation between the value of the index and the extent of wilting.

During the summer of 1914 it was again the writer's privilege to carry out studies in this connection at the Desert Laboratory, and he wishes here to express his appreciation of the kindness of Dr. D. T. MACDOUGAL, director of the Department of Botanical Research of the Carnegie Institution, in placing at his disposal the facilities of the Laboratory. At the suggestion of

[5] ALWAY, A. J., Studies on the relation of the non-available water of the soil to the hygroscopic coefficient. Nebraska Agric. Exp. Sta. Research Bull. 3. 1913.

[6] BAKKE, A. L., Studies on the transpiring power of plants as indicated by the method of standardized hygrometric paper. Jour. Ecol. 2:145–173. 1914 (see pp. 166–168).

Professor B. E. LIVINGSTON, an attempt was made to obtain further information concerning the march of the wilting process by means of cobalt chloride paper and the index of foliar transpiring power.

Various writers have shown that the transpiration rate falls suddenly with wilting, but rises again thereafter to a considerable extent, subsequently to fall once more as desiccation finally occurs. It appeared that these alterations in the transpiration rate must be due to internal conditions (within the plant), and that a similar march should be shown by the value of the index of transpiring power. To test this supposition, sunflower plants (*Helianthus annuus* L.) were lifted from the open soil in the forenoon, the adhering soil was shaken from the root system, and the plants were allowed to wilt in the laboratory. The temperature of the room was about 32° C. and varied but little during the experiments. Determinations of the index of transpiring power for both the upper and lower leaf surfaces were made at hourly intervals, the first determination just preceding the lifting of the plant.

An example of the sort of results obtained is given in table I. Five leaves of different ages were employed, the same leaves being tested at each time of observation. Although there were considerable differences in the indices for different leaves at any one time, according to their various ages or positions upon the plant, all five indices have been averaged to give a single index for each time. The first observation was made just before the plant was lifted from the soil. No wilting was apparent at this time. The last observation was made after drying of the leaves became pronounced. It required 10–15 minutes to complete each observation, the tests being begun at the time indicated in the table.

From the data given in table I it is at once clear that the indices first decrease rapidly, then increase, and then decrease again. This march for the upper and lower surfaces is shown graphically in fig. 1, where abscissas denote time and ordinates denote index values which are shown upon the graphs.

Wilting began almost immediately after the removal of the plant from the soil. The indices are seen to decrease very rapidly during the first hour. This first rapid decrease is followed by a continued but very gradual decrease during the four following

hours. Then a marked increase in the index values is evident, lasting for two hours, after which another decrease is clearly shown.

TABLE I

MARCH OF THE INDEX OF TRANSPIRING POWER FOR UPPER, LOWER, AND ENTIRE LEAF SURFACE OF UPROOTED PLANT OF *Helianthus annuus* L. DURING PROGRESSIVE WILTING AND DRYING OF THE LEAVES

TIME OF OBSERVATION	INDEX OF FOLIAR TRANSPIRING POWER		
	Lower surface	Upper surface	Entire surface
8:30.....	0.9468	0.9020	0.9243
9:30.....	0.1175	0.1289	0.1232
10:30.....	0.1054	0.0865	0.0959
11:30.....	0.0632	0.0699	0.0665
12:30.....	0.0657	0.0616	0.0636
13:30.....	0.0571	0.0578	0.0574
14:30.....	0.1029	0.1013	0.1021
15:30.....	0.1723	0.2029	0.1876
16:30.....	0.0899	0.1216	0.1058

To interpret these alterations in the index values, it may safely be supposed that the great initial fall in the graphs represents the prompt increase in incipient drying[7] within the leaves, which must have followed the uprooting of the plant and the consequent breaking of its connection with the soil moisture films.[8] Temporary wilting had already set in before the end of the first hour.

After wilting began, the increase in incipient drying apparently continued, but at a low rate, as indicated by the gradual downward slope of the graphs for the hours 9:30 to 13:30. During this time it may be supposed that the continuous water columns[9] of the plant remained mainly intact, so that the leaves were still slowly drawing water from the stem. With increasing tension on these

[7] LIVINGSTON, B. E., and BROWN, W. H., Relation of the daily march of transpiration to variations in the water content of foliage leaves. BOT. GAZ. **53**:305–330. 1912.

[8] BROWN, W. H., The relation of evaporation to the water content of the soil at the time of wilting. Plant World **15**:121–134. 1912; CALDWELL, J. S., *loc. cit.*

[9] DIXON, H. H., Transpiration and the ascent of sap. Prog. Rei Bot. **3**:1–66. 1909; RENNER, O., Experimentelle Beiträge zur Kenntnis der Wasserbewegung. Flora **103**:171–247. 1911.

water columns the incipient drying of the leaves should be increased, which should in turn lower the transpiring power.

The relatively high transpiring power indicated for the hours 14:30 and 15:30 appears to have followed the breaking of the water columns, by which the entire water mass of the plant had previously been united. Such a breaking should remove the tensile strain from the leaf cells, decreasing the saturation deficit of their exposed cell walls and increasing their transpiring power. From the time when this rupture occurred, the removal of water from the leaves should be accompanied by air entrance and no further tensile strength could be developed. If this is the correct interpretation of the observation here set forth, the rupture of the water columns extended over the period from 13:30 to 15:30, during which time the transpiring power was markedly increasing.

After hour 15:30, it is to be supposed that practically no more water entered the leaves from the stem, and the leaves gradually dried out, exhibiting the decreasing transpiring power which should accompany desiccation.

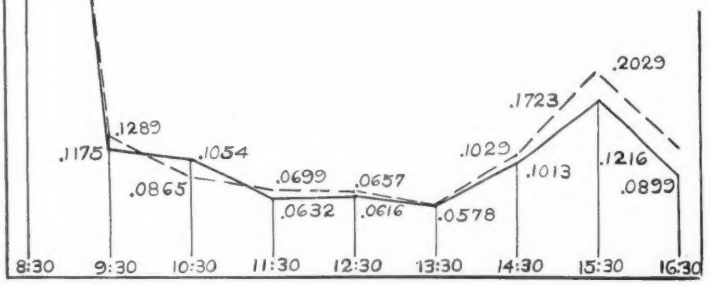

FIG. 1.—Graphs showing march of index of foliar transpiring power for wilting sunflower plant: lower leaf surface full line; upper leaf surface broken line.

From the nature of permanent wilting, and from the theoretical considerations above stated, it appears highly probable that this

stage of wilting represents simply the *most intense wilting possible without serious rupture of the water columns of the plant.* At any rate, this rupture should represent a rather definite critical point in the march of the power of the plant to extract water from the soil, probably the same critical point about which the concept of permanent wilting has been developed. If this suggestion be correct, then the graphs of fig. 1 show that this critical point occurred in the particular case under discussion about hour 13:30, or five hours after the roots actually ceased to absorb moisture from the soil. In other words, it appears that the plant in question probably attained the stage of permanent wilting about five hours after it was uprooted and taken into the laboratory.

To test the validity of this supposed relation between the minimum in foliar transpiring power and the attainment of permanent wilting, it will of course be necessary to employ the hygrometric paper tests upon plants in which permanent wilting is subsequently established by the method of BRIGGS and SHANTZ—the 24-hour exposure to a saturated atmosphere, the plants being still rooted in the soil. The press of other experimentation prevented the writer from undertaking this comparison, and the foregoing suggestions have been made with the hope that such a study as that just mentioned may be accomplished at no distant time. Enough has been done to render it highly probable that the index of foliar transpiring power determined by means of cobalt chloride paper may furnish a somewhat precise criterion for the determination of that state of plants heretofore vaguely defined as permanent wilting.

IOWA STATE COLLEGE
AMES, IOWA

BRIEFER ARTICLES

A TROPISM CHAMBER

(WITH THREE FIGURES)

A few years ago the writer planned some classroom experiments to illustrate the geotropism of roots. The students wasted much time and many seedlings because of the wilting of the roots while they were transferring them to the observation chambers and fastening them to their supports. To overcome this difficulty some special tropism chambers were designed. These have given excellent satisfaction, and have proved to be so well adapted to the study of tropic responses that their use has suggested a number of new classroom experiments, which would have been impracticable without this apparatus.

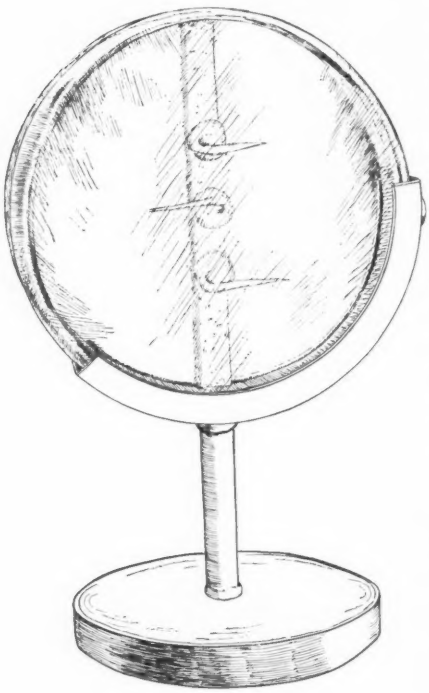

FIG. 1

The first makeshift contrivance consisted simply of a Petri dish, 4–5 inches in diameter, with a small piece of cork cemented to the bottom, near one side. The dish was partly lined with wet filter paper. The seedling was pinned to the cork and the dish set on edge on top of an ordinary tumbler. The curvature of the top of the tumbler made a convenient support for the cover of the Petri dish. The Petri

dish could be rotated and the radicle of the seedling quickly brought to any desired angle with the vertical.

The makeshift apparatus served the purpose fairly well, but the tumbler support was not always convenient. A special support was then constructed. As will be seen from the drawings, the support consists of a circular trough (of brass) mounted on a pedestal. There are two sockets for attaching the trough to the pedestal, which screws into the socket. These sockets are 90° apart. The purpose of the extra socket is shown in fig. 2, where the tropism chamber is shown attached to a regular laboratory support. This arrangement is for use with the horizontal microscope.[1] The chamber may be transferred from the base to the laboratory support without altering the position of the seedling.

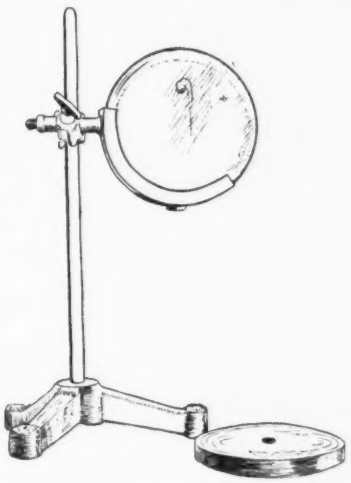

FIG. 2

Fig. 1 shows the chamber provided with a strip of cork so as to make room for several seedlings. The drawing is from an experiment to illustrate traumatropism.

Fig. 3 shows the improved apparatus. The support is provided with a scale marked in degrees. This makes it possible to place the seedling at any desired angle with the vertical. Four marks etched or scratched on the cover of the Petri dish 90° apart serve as pointers. Into a hole, bored through the bottom of the Petri dish, a cork is inserted. The seedling is pinned to the inner face of the cork. The cork can be moved from the outside and it is possible, therefore, to make the final adjustments of the position of the seedling (for example, bringing the radicle parallel with the faces of the chamber) without opening the Petri dish.

[1] The tube from any compound microscope, clamped to a laboratory support, will serve as a horizontal microscope. A hair stuck to the diaphram in the eyepiece will serve as a cross-hair.

The bottom of the Petri dish is ruled into 5 mm. squares. The squares not only aid in determining the angles made by the bending root, but also serve as markers to locate the regions of growth and curvature. A sheet of coordinate paper pasted over the bottom of the dish will serve nearly as well as the cross-ruling. Thin paper, such as is used for making blue-print tracings, is best. The paper can be made more transparent by wetting it with a mixture of alcohol, glycerine, and water.

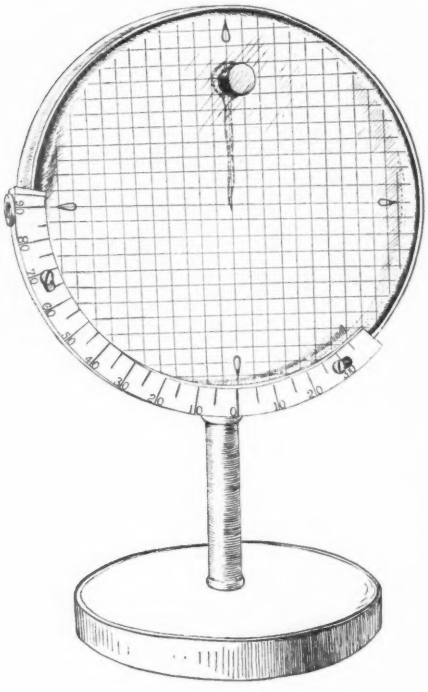

FIG. 3

Seedlings may be grown for a number of days in the chambers. It is possible, therefore, to place the seedlings in the chambers some time previous to the time set for the experiments. If the filter paper lining the chamber is placed symmetrically, so as to avoid hydrotropic curvatures, the radicles will grow straight downward. The chamber can now be rotated and the seedling quickly brought to any desired angle with the vertical, and without exposing it to the dry air of the laboratory. The chambers are excellent for experiments on perception and latent periods, and for periodic responses.—W. T. BOVIE, *Laboratory of Plant Physiology, Harvard University.*

CURRENT LITERATURE

NOTES FOR STUDENTS

The "graft hybrids" of Bronvaux.—Since the work of WINKLER in producing so-called "graft hybrids" among several species of *Solanum*, the older chimeras, *Laburnum Adami* and the "Crataegomespili of Bronvaux" have attracted renewed attention. The graft hybrids of Bronvaux originated from the callus formed at the junction between a *Crataegus monogyna* stock and a scion of *Mespilus germanica*. These aberrant branches were of two types, and have been described under the names *Crataegomespilus Asnieresii* and *Crataegomespilus Dardari*. The first of these resembles more closely *Crataegus monogyna*, while the *Crataegomespilus Dardari* has a much closer resemblance to *Mespilus*. A thorough study of these two chimeras has been made by MEYER,[1] in order to find means of identifying the tissues which have been derived from the two parent species. In most respects the tissues of *Crataegus* and *Mespilus* are so similar that few distinguishing features can be found. Numerous chemical tests failed to discover any method for certainly differentiating the tissues of the two species. A study of the chromosomes, however, gave one good criterion, for, although the number of chromosomes in the two species is the same (32 in the diploid nucleus), the chromosomes of *Mespilus germanica* are considerably longer and thinner than those of *Crataegus monogyna*. The capacity to produce anthocyan, which is present in the epidermis of the fruits of *Crataegus*, is lacking in the fruits of *Mespilus*, while the reverse relation with respect to anthocyan is seen in the fact that *Mespilus* flowers turn reddish in aging, while those of *Crataegus* remain white. The fruits of the two chimeras show no anthocyan, and the flowers of both turn reddish with age.

The only clear distinction that could be found in the internal anatomy of the two species was visible only in longitudinal sections. The libriform vessels in *Mespilus* possess spiral thickenings which are absent in those of *Crataegus*. In both chimeras the libriform vessels lack spiral thickenings. The form of the epidermal cells is also strikingly different in the two species, those of *Mespilus germanica* being oblong, while those of *Crataegus* are nearly spherical. The cuticle of *Crataegus* is level, while that of *Mespilus* follows the contour of the rounded ends of the underlying cells. The epidermis of both chimeras agrees with that of *Mespilus*. The fruits of *Mespilus* are five-loculed and those of *Crataegus* one-loculed. Both of the chimeras have one-loculed fruits.

[1] MEYER, J., Die Crataegomespili von Bronvaux. Zeitschr. Ind. Abstamm. Vererb. **13**:193–233. 1915.

The view of BAUR is sustained throughout, that these two "graft hybrids" consist of a core of *Crataegus* tissue overlaid by a mantle of *Mespilus*. In *Crataegomespilus Asnieresii* the mantle is the single epidermal layer, while in *C. Dardari* the first subepidermal layer is also of *Mespilus* tissue. By periclinal divisions this subepidermal layer may come to be represented by a number of cell layers, *Mespilus* chromosomes having been identified as deep as the eighth cell layer in one case. As the initiation of lateral branching results from periclinal divisions in the second subepidermal layer, the author argues that no chimera would be able to maintain itself as a chimera in which the mantle should consist of more than two layers. Several "reversions" to one or the other component species, and changes from one of the chimeras to the other, are described and easily explained, and one sectorial branch is figured and described.—G. H. SHULL.

Albinism in maize.—The important studies of EMERSON[2] on the inheritance of albinism and partial albinism in maize have been continued by one of his students.[3] Two different forms of albinism are found, one in which the seedlings are pure white, the other in which they are yellowish white, the latter turning slightly greenish as they grow older and sometimes developing enough chlorophyll to reach maturity. Both of these sorts of albinism prove to be simple Mendelian recessives to the normal green stains. The pure white seedlings could not be used in breeding, but the yellowish white supplied several mature plants which were selfed and which gave progenies consisting entirely of yellowish white seedlings. When plants heterozygous for the pure white were crossed with plants heterozygous for yellowish white, all of the offspring were green, showing that the normal green plants possess two determiners, the absence of one of which gives rise to pure white seedlings, while the absence of the other gives yellowish white seedlings. In confirmation of this interpretation, the second generation from these crosses between the heterozygous plants consisted of four different kinds of families: (*a*) all green; (*b*) green and pure white in the ratio 3:1; (*c*) green and yellowish white in the ratio 3:1; and (*d*) green, yellowish white, and pure white in the ratio 9:3:4. These results demonstrate the existence of the same genotypic situation in maize that NILSSON-EHLE[4] assumed to be present in rye in which pure white and yellowish white albinos were also found.

A continuation of the work on yellowish green (chlorina) plants described by EMERSON confirmed that investigator's conclusions that the yellowish

[2] EMERSON, R. A., The inheritance of certain forms of chlorophyll reduction in corn leaves. Rep. Nebr. Agric. Exp. Sta. **25**:89–105. 1912.

[3] MILES, F. C., A genetic and cytological study of certain types of albinism in maize. Jour. Genet. **4**:193–214. *pl. 1.* 1915.

[4] NILSSON-EHLE, H., Einige Beobachtungen über erbliche Variationen der Chlorophylleigenschaft bei den Getreidearten. Zeitschr. Ind. Abstamm. Vererb. **9**:289–300. 1913.

green is a simple Mendelian recessive to the normal, and a similar result was obtained in crosses between the striped forms known as *Zea japonica*, in crosses with the normal green strains, the striped being recessive to normal, though in the latter cross there is some confusion when certain differences in aleurone colors are also involved in the same cross. The exact nature of this relation between aleurone colors and leaf colors was not worked out. Crosses between striped plants and chlorina, and between striped and yellowish white yielded in each case normal green plants, owing to the bringing together of complementary factors.

MILES also made a study of the chloroplasts in the several strains with which he worked. He could find no plastids in the pure white seedlings, and only a few small plastids in the yellowish white, which became more numerous and larger as the plants grew older, until they resembled, in the better developed individuals, the normal condition. In the case of striped-leafed plants, the arrangement of the plastids showed a sharp distinction between the cells of the green portions of the plants and those of the white stripes.—G. H. SHULL.

The physiology of pollen.—In his work on the physiology of pollen, TOKUGAWA[5] dealt with three main points of interest: factors determining germination, factors determining the direction of the pollen tube, and factors determining the rate and extent of the growth of the pollen tube. The investigator adds evidence against the views of MOLISCH and of BURCH that specific substances on the stigma generally determine whether the pollen will germinate or not. Already many cases have been found in which the physical conditions are the important ones in determining germination. JOST showed for various species in several families that restricted water supply is the main requirement for the germination of the pollen. He secured this condition by germination of the pollen in a saturated atmosphere or on leaf epidermis or parchment paper. TOKUGAWA adds many more to the list. He has evidently failed, however, to notice the work of MARTIN,[6] which shows the important newly discovered fact that conditions giving a free water supply to the stigma may lead to sterility. This holds for alfalfa and certain clovers in the central Mississippi Valley when pollination occurs at moist or wet periods.

The author confirms the statement that sugars and proteins are important chemotropic substances for the pollen tube. In certain plants (*Narcissus Tazetti* and *Prunus mume*) sugars are effective, and in other (*Camellia japonica*) proteins. He concludes that chemotropism determines the entrance of the tube into the stigma canals and the micropyle, and that the tube is directed in a physical manner in the rest of its course.

The conditions affecting growth of the pollen tube are considered in relation to their significance in determining self-sterility and failure to

[5] TOKUGAWA, Y., Zur Physiologie des Pollens. Jour. Coll. Sci. Tokyo **35**:1–35. *figs.* 2. 1914.

[6] BOT. GAZ. **56**:112–126. 1913.

hybridize. In this connection it is found that tubes penetrate rather deeply into agar. The work with several species of lilies shows that the tubes penetrate most rapidly in stigmas of the same species, and progressively slower as the species becomes more distant. When the tube penetration was slow in these crosses, it became continuously slower as the depth of penetration increased, and finally ceased short of the embryo sac. The writer thinks that he has shown that this behavior is due to shortage of nutrient or stimulative materials and not due to toxic materials. His evidence, however, is not at all against the gradual formation of antibodies, a suggestion made by JOST. Self-sterility and failure to hybridize, so far as it is due to lack of tube penetration, deserves a thorough physiological study in the light of our modern knowledge of antibodies and of several other phases of physiology. The later evidence (perhaps not entirely conclusive) that the character of self-sterility mendelizes does not subtract in the least from the need of such an exhaustive physiological study.—WILLIAM. CROCKER.

A new type of embryo sac.—The evolution of the sporophyte and the gradual reduction of the gametophyte are well known to every botanist. In the angiosperms, where the reduction of the gametophyte generation is most extreme, intensive research has revealed several types of embryo sac. Doubtless the most common type and the one long believed to be practically the only type is the familiar 8-nucleate sac, two of whose nuclei fuse to form the endosperm nucleus. This sac is formed by one of a row of 4 megaspores. Soon the *Lilium* type, looking like the preceding but formed from 4 megaspores, was discovered. Sacs with 16 nuclei, some formed from four megaspores and some from a single megaspore, were added to the list. *Cypripedium* has a 4-nucleate sac formed from two megaspores. Since the discovery of the *Cypripedium* type, other 4-nucleate sacs have been found, some formed from one megaspore and some from two.

A new type of embryo sac has been found in *Plumbagella*, one of the Plumbaginaceae.[7] The development starts as in *Lilium*, there being 4 megaspores, not separated by walls, but there are no further nuclear divisions. One nucleus becomes the nucleus of the egg, two fuse to form an endosperm nucleus, and the remaining nucleus, which is at the antipodal end of the sac, disintegrates. At the time of fertilization, there are only two nuclei in the sac. The most important feature is that a megaspore functions directly as the egg. The fusion of two megaspore nuclei to form an endosperm nucleus is also new. Without question, this is the most reduced female gametophyte ever described, and in the nature of the case the reduction can go no farther. DAHLGREN recognizes that the reduction is as extreme as in animals, and he compares this sac with the egg and three polar bodies.

[7] DAHLGREN, K. V. OSSIAN, Der Embryosack von *Plumbagella*, ein neuer Typus. Arkiv für Botanik **14**:1–10. *figs.* 5. 1915.

Ten years ago, in a paper on alternation of generations in animals,[8] the reviewer predicted that gametophytes more reduced than those known at that time might still be found. Miss PACE soon described the *Cypripedium* type and afterward various investigators found digressions from the "normal" type in *Peperomia*, *Penaea*, *Oenothera*, *Clintonia*, *Lawia*, *Podostemon*, *Dicraea*, *Helosis*, and *Plumbagella*.

It is interesting to note that the most reduced sac has not been found in the most advanced family. It has been a prevalent custom for investigators to focus their attention upon forms which at the moment seemed to have particular phylogenetic significance, forgetting not only that phylogenetic schemes might be awry, but also that facts of great importance in interpreting phylogeny might be found in plants not in the supposed line of ascent.—C. J. CHAMBERLAIN.

Phytopathology in the tropics.—Dr. JOHANNA WESTERDIJK presented a paper at the twenty-fifth anniversary celebration of the Missouri Botanical Garden[9] dealing with the general facts concerning plant diseases in the tropics, based upon recent observations she had made in the Dutch colonies of the East Indies. The combination of high temperature and moisture would seem to be peculiarly favorable to fungi, and therefore to diseases of economic plants induced by fungi; but in fact there are only a few such diseases of real importance. Not only among cultivated plants, but also among the native plants are attacks of fungi rare. Dr. WESTERDIJK has concluded that the tropical temperature is too high for many fungi, a conclusion confirmed also by experimental work. The condition of the tropical host is also unfavorable for invasion by fungi because of the high water content and small air content of the tissues concerned. Among the disease-producing fungi in the tropics, mention is made of the root fungi (certain Hymenomycetes) which attack practically all cultural woody plants. The fungi (certain Ascomycetes and Fungi Imperfecti) inducing die-back diseases of orchards and forests, so common in temperate regions, are represented in the tropics only by a *Corticium* (a Hymenomycete); and there are no representatives of the powdery mildews (Erysiphaceae). The relation of fungus attacks to temperature is well shown in the behavior of *Phytophthora infestans* in Java, where potatoes are cultivated in mountain districts between 1500 and 6000 feet altitude. In the lower areas the infected regions are rare, but in ascending to the higher areas of lower temperature, the more destructive does *Phytophthora* become. Among the rusts there is only one representative of importance in tropical agriculture, namely the coffee leaf disease (*Hemileia vastatrix*). Leaf spot diseases are much less frequent than in Europe or in the United States; while bacterial

[8] BOT. GAZ. **39**:137–144. 1905.

[9] WESTERDIJK, JOHANNA, Phytopathology in the tropics. Annals Mo. Bot. Gard. **2**:307–313. 1915.

diseases are scarcely to be found. The general conclusion is that the small part which fungi play in the plant diseases of the tropics is not due to the absence of fungi, but the tropical conditions that influence the hosts in their relation to parasites.—J. M. C.

Soil acidity.—DAIKUHARA[10] finds that more than 75 per cent of the soils of Japan and Korea are acid, while the Chinese, South Oceanic, and European soils show little or no acid. This is due to the difference in geological formations, climatic conditions, and fertilization methods. Soils of acid rock origin show the most prevalent acidity, those of basic origin less, and those of laval ash are generally free from acids. Mesozoic formations are most commonly acid; tertiary, paleozoic, and diluvial next; and alluvial formations least. The condition in Japan and Korea is related to the common occurrence of acid soils in the United States. The author finds that more than half of the cases of acidity are due to aluminium and iron compounds of acid reaction that are adsorbed by the colloids of the soil and set free upon the addition of such fertilizer salts as KCl, K_2SO_4, KNO_3, and NaCl. In these soils fertilizing with neutral salts alone often proves very detrimental, but fertilizing with neutral salts plus lime is highly beneficial. More than 50 per cent of the cases of soil acidity in Japan and Korea are due to this colloidal phenomenon. The author cites from mineralogies a number of iron and aluminium compounds that are acid in reaction, as phosphates, double salts of silicates, etc. It was already known that negative colloids of the soil often render lime-poor soils acid by adsorbing the basic ion of neutral salts and setting free the acid. The author speaks of his finding as a newly discovered source of soil acidity. He has developed a test for soil acidity that shows advantages over the litmus, Baumann and Gully, or the Loew tests. He has also evolved a method for the quantitative determination of soil acidity. The acid soils generally bear little lime, and the lime factor is unfavorable, owing to the excess of magnesium.

We are now coming to recognize that many acid-forming processes take a part in the dissolution of lime from the soil and the final rendering of it acid. The two absorption processes described above are only two of the several known.[11]—WILLIAM CROCKER.

Field physiology of cotton.—BALLS and HOLTON[12] have published an article on analysis of agricultural yield which exemplifies the application of

[10] DAIKUHARA, G., Über saure Mineralböden. Bull. Imp. Cent. Agr. Exp. Sta. Japan **2**:1–40. 1914.

[11] Readers will be interested in the following citations from American literature, in addition to the literature in the foregoing paper: HARRIS, J. E., Soil acidity and methods for its detection. Science N.S. **40**:491–493. 1914. TROUG, E. A., A new method for the determination of soil acidity. Science N.S. **40**:246–248. 1914. BARKER, J. F., and COLLISON, R. C., Ground limestone for acid soils. Bull. 400. Geneva Exp. Sta. New York. 1915.

[12] BALLS, W. L., and HOLTON, F. S., Analysis of agricultural yield. Part I. The spacing experiments with Egyptian cotton, 1912. Phil. Trans. Roy. Soc. London B **206**:103–180. 1915.

very accurate scientific methods to the problem of crop yield. The work, with its excellent analytical methods, deserves the careful attention of students of field crop production. When such methods are in general use in this phase of agronomy, the results and conclusions gained will carry with them much more weight and dependence. One is especially impressed with daily determinations of growth rate and flower and boll opening, which make possible the evaluation of accidental and temporary factors. Aside from the important contribution to method in analysis of agricultural yield, which after all is its greatest value, the article also contributes some clear-cut conclusions upon spacing as effecting production in the Nile valley, as follows: "(*a*) the experiment shows that the yield of a cotton crop is primarily dependent on the number of flowers which it forms; (*b*) the normal extension of the root system of an isolated cotton plant can utilize more than 2 m.² of soil surface in soil which is more than 2 m. deep; (*c*) the plants in the field crop have only 0.18 m.² allowed them or less; most of the phenomena of field crop physiology in the fruiting seasons are traceable to the interference of one root system with another; (*d*) the yield per unit area of the conventional spacing of the Egyptian Fellah is the maximum obtainable under the limitations of field cultivation (two plants per hole, each hole 0.34 m.²); (*e*) the sources of error in field experiments with cotton can be traced to (1) soil variation, especially below one meter depth; (2) insufficient frequency of observation, whereby accidental episodes cannot be distinguished from normal sequences; (3) fluctuations of single plants, heterogeneity of commercial varieties, and normal physiological variations from day to day."—WILLIAM CROCKER.

Geotropism of the grass node.—It is well known that lodged grass stems recover their vertical position by growth on the lower flank of the older mature nodes. Gravity, acting transversely on the stem rather than longitudinally, incites growth in these otherwise mature regions of the stem. ELFVING showed that these nodes are incited to growth when the stems are rotated with transverse exposure on the clinostat, thus giving a diffuse all-sided action of gravity; but in this case growth is equal on all flanks and no bending results. RISS[13] has attempted to analyze more fully the mode of action of gravity in this behavior. She finds that when the gravity stimulus is applied intermittently but equally (intermittent clinostat) on two opposite flanks, the growth is greater than when it acts equally (continuous clinostat) on all flanks. By means of a compound centrifuge clinostat,[14] she has applied a centrifugal stimulus of one gravity transversely (intermittently and continuously as above), at the same time the organ held its vertical position in relation to the pull of gravity. While the transverse stimulus thus applied incites growth, its effect is far less than in the absence of the longitudinal pull of gravity.

[13] RISS, M. M., Über den Geotropism der Grasknoten. Zeitschr. Bot. **7**:145–170. 1915.

[14] See BOT. GAZ. **58**:89. 1914.

She finds no conclusive evidence for or against the view that the tropic and growth stimuli of gravity in this organ are distinct. Her work makes it evident that the lack of growth in the older nodes with the stem vertical is due both to the lack of the stimulating transverse action of gravity, and to the presence of the inhibiting longitudinal action. Thus we see these responses to stimuli becoming more and more complex. One wonders whether a study of changes, acid and otherwise, induced in the tissues of the nodes by these various exposures might not simplify the matter. Such, I believe, is the possibility of real progress in this field.—WILLIAM CROCKER.

Phylogenetic significance of endosperm.—Nuclear endosperm and cellular endosperm, and also endosperm beginning its development with a free nuclear period and later passing into a cellular condition, have been known since the days of HOFMEISTER; and since that time various modifications and peculiarities have been described, some of them characterizing genera or families or even orders; while others seem to be confined to species. Whether the character of the endosperm has any phylogenetic significance or not, is a question which has often been discussed and often answered, both in the affirmative and in the negative.

The most recent discussion[15] is also the most comprehensive. It is a study of the literature rather than a laboratory investigation. For all the orders of Dicotyledons and Monocotyledons, the literature dealing with the endosperm has been assembled and discussed and charts have been made, so that it is possible to see at a glance just what the endosperm and haustorium conditions are in any order. In this bird's-eye view, the names of the principal investigators are given and full citations appear in an extensive bibliography. After describing the endosperm and haustorium situation in each order, often treating the families separately, sometimes the genera, and occasionally the species, the author adds a long summary dealing with orders. Both in the introduction and in the conclusion it is very plainly stated that the endosperm character is only one factor among many, but nevertheless endosperm and haustoria characters have great phylogenetic significance.—CHARLES J. CHAMBERLAIN.

Temperature and photo-perceptions.—In studying the influence of temperature upon phototropism in the coleoptile of *Avena sativa*, Miss DEVRIES[16] has determined the influence of temperature upon the rate of photo-perception and photo-reaction and the influence of previous heating upon the rate of these processes. She finds that van't Hoff's law of rate of chemical reaction

[15] JACOBSSON-STIASNY, EMMA, Versuch einer phylogenetischen Verwertung der Endosperm- und Haustorialbildung bei den Angiospermen. Sitzungsb. Kaiserl. Akad. Wiss. Wien **123**:1–137. 1914.

[16] DEVRIES, M. S., Der Einfluss der Temperatur auf den Phototropismus. Extrait du Rec. Trav. Bot. Néerland. **11**:195–291. *figs.* 7. 1914.

applies to photo-perception, with a coefficient of about 2.6 for 10° C. rise in temperature up to 30° C. It also applies to photo-reaction with a considerably smaller coefficient. Above 30° C. an injurious time effect of high temperature sets in, and finally at 40° C. the power of perception and response is soon lost. These results stand in contradiction to those of NYBERGH, who claimed that temperature ranging from −3° C. to 47° C. have little influence upon the photo-perception rate, indicating that the process is a strictly photo-chemical reaction such as occurs on the photographic plate. DEVRIES' work, on the other hand, lines these two processes up, so far as they are influenced in rate by temperature, with chemical reactions in homogeneous solutions in general, and with photosynthesis, respiration, and geo-perception.[17] From 0° to 25° C. the perception speed was independent of the time of previous warming. Long previous warming at 27.5–30° C. hastened perception rate, and such previous heating at 32.5° C. or higher temperatures slowed the perception rate. One hour's heating at 39° C. lowered the perception speed at 20° C. more than four-fold. This effect entirely disappeared, however, after four hours' storage at 20° C., and is therefore considered rather a matter of hysteresis than of the accumulation of poisonous materials.—WILLIAM CROCKER.

Invasion of a prairie grove.—In the high prairie just outside of Lincoln, Nebraska, a grove was started about forty years ago by running furrows at intervals of 4–6 feet through the prairie and dropping the tree seeds into the furrows. At present about 20 acres are thus forested with *Fraxinus pennsylvanica*, *Juglans nigra*, *Ulmus fulva*, *Acer saccharinum*, and *A. Negundo*. No culture has been attempted at any time during the history of the grove, nor has there been any damage by fire or grazing, hence the forested area affords an exceptionally good demonstration of the fact that trees grow freely once they are planted in this prairie soil, although they almost never invade the grasslands, and it also provides an unusually good opportunity of studying the changes in the undergrowth vegetation resulting from the changed conditions due to the tree growth. POOL[18] in investigating the character of the invasions has found that not only has the prairie sod gone, but nearly every one of the original prairie species has entirely disappeared, being replaced by some 90 invading species, of which 85 per cent are mesophytic and 60 per cent are distinctly woodland. Lists of these species prove how completely the area has been transformed from prairie to forest in a very short period. Doubtless changes in soil moisture, evaporation intensity, and light as the trees developed led to the changes in the undergrowth. POOL has these and other factors under investigation and doubtless his results will form a valuable contribution to the understanding of the problems of the relations existing between the grasslands and the forests.—GEO. D. FULLER.

[17] BOT. GAZ. **50**:233–234. 1910; **51**:239. 1911.

[18] POOL, R. J., The invasion of a planted prairie grove. Proc. Soc. Amer. For. **10**:1–8. 1915.

Embryology of the Rosaceae.—A literary study of the embryology of the Rosaceae brings JACOBSSON-STIASNY[19] to some conclusions in regard to the interrelationships of the subdivisions of this large family. The characters which were traced through the various forms are number and character of integuments, number of archesporial cells and megaspores, number of tapetal cells, presence or absence of an obturator, character of young and mature endosperm, fate of the nucellus, character of the suspensor, orientation of the ovule, and form of the embryo. After tabulating and comparing all these features, the author concludes that the Rosaceae do not represent a single developmental line, but that the Spiroideae are the primitive stock which has produced two principal lines, one consisting of the Pomoideae and Prunoideae, and the other of the Rosoideae.

While everyone recognizes that in an investigation of such scope it would be impossible to make a laboratory study of all the forms, still those who are familiar with such investigations realize that descriptions are not always reliable, and that observations upon embryology, made before technique had reached its present efficiency, may be quite misleading. However, such an assembling of the literature and the graphic presentation of the results will be useful to workers in various fields.—CHARLES J. CHAMBERLAIN.

Growth forms.—On the basis of RAUNKIAER'S classification of growth forms, TAYLOR[20] has made an interesting analysis of his own *Flora of the vicinity of New York*, both as a whole and as to certain of its constituent elements. He notes the high percentage of water plants and of perennials possessing rootstocks and bulbs; and calls attention to the much greater abundance of woody forms among the southern types in the flora than among the northern ones. The "biological spectrum" of growth forms in the region covered is compared with spectra of several other areas, arctic, temperate, and tropical, and certain conclusions as to climate are suggested. Such a method of studying climate as this of RAUNKIAER'S, by rigid comparative analyses of the floras of widely separated regions, seems to be open to the general objection that it underestimates the importance of the historical factor. Temperate areas of the Northern Hemisphere, for example, contain a much higher proportion of herbaceous species than do regions with a corresponding climate south of the equator, presumably owing to the fact that the herbaceous type has originated for the most part in the north temperate zone. Such careful analyses of growth habit as the present one, however, are of much value for drawing critical comparisons between floras, and for other purposes. It is to be hoped that their number will continue to increase.—E. W. SINNOTT.

[19] JACOBSSON-STIASNY, EMMA, Versuch einer embryologisch-phylogenetischen Bearbeitung der Rosaceae. Sitzungsb. Kaiserl. Akad. Wiss. Wien **123**:1–38. 1914.

[20] TAYLOR, N., The growth forms of the flora of New York and vicinity. Amer. Jour. Bot. **2**:23–31. 1915.

Modification of germ plasm.—In connection with the twenty-fifth anniversary celebration of the Missouri Botanical Garden, MACDOUGAL[21] has published an account of the work done at the Desert Laboratory of the Carnegie Institute in experimental modification of germ plasm. It is directed against the old conception of "an inviolable germ plasm," in the interest of the conception that germ plasm is a responsive structure, with its chemistry and physics. At the Desert Laboratory over 200 species of seed plants, selected for their suitability and promise of response, have been included in the cultures, subjected to various conditions (mountain top, desert, and seashore). Less than 80 of these have survived, and about 20 continued in all three habitats. The notable feature in the behavior of these plants in unaccustomed habitats is the variation in sexual reproduction and seed formation. A second method of experimentation has been to use "inciting agents" applied directly to the reproductive bodies. In this kind of experimental work the forms chiefly used at the Desert Laboratory were certain cacti, *Penstemon Wrightii*, and an undescribed species of *Scrophularia*, the results reported in the paper being chiefly obtained from the last form. The paper concludes with a condensed statement of the conditions involved in any experimental work upon the germ plasm.—J. M. C.

Bacterial diseases of plants.—SMITH,[22] in a paper presented at the twenty-fifth anniversary celebration of the Missouri Botanical Garden, has summarized our present knowledge in reference to the bacterial diseases of plants, all of which has come within a generation. It is an interesting historical fact that our first knowledge of such diseases was the announcement by BURRILL in 1878 that pear blight is a bacterial disease. SMITH states that he is now ready to venture the sweeping statement that eventually a bacterial disease will be found in every family of plants, from the lowest to the highest. At present such diseases are known to occur in 140 genera, representing more than 50 families. The paper includes a list of the families of seed plants, those in which bacterial diseases have been found being indicated. There is also discussion of the following interesting topics: period of greatest susceptibility; what governs infection; how the infection occurs; time between infection and appearance of the disease; recovery from disease; agents of transmission; extra-vegetal habitat of the parasites; action of the parasites on the host; the reaction of the host; prevalence and geographic distribution; and methods of control.—J. M. C.

Stem anatomy of Isoetes.—LANG has begun an investigation of *Isoetes*, whose problems, as he remarks, remain difficult and fascinating. The first

[21] MACDOUGAL, D. T., The experimental modification of germ plasm. Annals Mo. Bot. Gard. **2**:253–274. *figs. 4.* 1915.

[22] SMITH, ERWIN F., A conspectus of bacterial diseases of plants. Annals Mo. Bot. Gard. **2**:377–401. 1915.

paper[23] deals with the morphological nature of the so-called stem, which he calls "stock," the reason being that one of the questions is whether this tuberous axis represents only a short stem. After a presentation of the anatomical details, LANG concludes that the stock consists of an upwardly growing shoot region, and a downwardly growing region giving rise to the roots; the latter region he calls the rhizophore. He suggests that the origin of the rhizophore may hold some relation to the deep-seated secondary meristem at the base of the shoot, but that, once initiated, "the growing region of the rhizophore behaves like the primary axis which is congenitally sunken and inclosed." This region, it seems, is very suggestive of the basal root-bearing region of *Lepidodendron* and its allies, and confirms WILLIAMSON'S suggestion that *Isoetes* may be the nearest living representative of that paleozoic stock.—J. M. C.

Phylogeny of the Ascomycetes.—ATKINSON,[24] in a paper presented at the twenty-fifth anniversary celebration of the Missouri Botanical Garden, discusses at length the vexed question of the origin of the Ascomycetes and their interrelationships. In general his thesis is that the Ascomycetes have been derived from the Phycomycetes, rather than from the red algae, the possible transitions being suggested most strikingly by such a form as *Dipodascus*. The details of the argument are too numerous to cite here, but it is well sustained, and more convincing than any argument hitherto favoring the algal origin of the group. A chart presents in graphic form the conclusions as to interrelationships, the Protoascomycetes arising from the Phycomycetes, and in turn giving rise to the Euascomycetes through the *Dipodascus* "stock." The divergent lines of the Euascomycetes are represented as emerging from two primitive overlapping stocks (*Gymnoascus* and *Monascus*). The paper is a very important contribution to our knowledge of a perplexing group.—J. M. C.

Cecidology.—One of the latest American papers on cecidia is by FELT,[25] in which the author describes a very large number of species of midges, many of which cause galls, while others are more or less closely associated with galls. Although this paper is primarily entomological, it contains many descriptions of galls which are of value to the botanist.

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[23] LANG, WILLIAM H., Studies in the morphology of *Isoetes*. I. The general morphology of the stock of *Isoetes lacustris*. Mem. and Proc. Manchester Lit. and Phil. Soc. **59**: no. 3. pp. 28. 1915.

[24] ATKINSON, GEO. F., Phylogeny and relationships in the Ascomycetes. Annals Mo. Bot. Gard. **2**:315–376. *figs.* 10. 1915.

[25] FELT, E. P., A study of gall midges II. Itonidinae. Rep. N.Y. State Entomol. 1913. pp. 79–211.

In the recent European literature we find a very interesting article by CHRISTY,[26] in which the author describes a gall previously unrecorded for the British Isles. It reaches its full size of 2–10 inches in length by the middle or end of May. It is a malformation of the pistillate flower and has the appearance of a bunch of moss. The same or a very similar gall due to *Eriophyes triadiatus* Napela is well known on the Continent, but thus far the author has failed to find the mites in the British forms. It appears to be somewhat similar to our American *Acarus aenigma* Walsh.—MEL T. COOK.

Anthocyan pigments in plants.—In an examination of the recent work upon the occurrence and chemical nature of the red, purple, and blue plant pigments known as anthocyans, and yellow pigments designated flavones or flavonols, EVEREST[27] has summarized the present state of our knowledge in a very concise manner. He shows that it has been established that (1) the anthocyans always occur as glucosides, and that some seven of these pigments have now been isolated; (2) the same pigment may be capable of showing a blue, purple, or red color, according as it exists as alkali salt, free pigment, or oxonium salt of some acid; all anthocyans do not, however, form blue alkali salts; (3) the anthocyans may be obtained from flavonols by reduction followed by spontaneous dehydration; and (4) glucosides of flavonols can pass, by reduction, to glucoside anthocyans without intermediate hydrolysis.—GEO. D. FULLER.

Morphology of Gnetum.—THOMPSON[28] has published a preliminary note on the embryo sac conditions in *Gnetum*, several species of which he has investigated. There are no vegetative cells in the male gametophyte, which is the expected contrast with *Ephedra*. Only free nuclei occur in the embryo sac before the pollen tube enters, although cells are formed before fertilization takes place, and one or more eggs are definitely organized. Perhaps the most significant observation is that before fertilization the female gametophyte becomes divided into a large number of multinucleate compartments, all the nuclei in each compartment later uniting to form a fusion nucleus, the endosperm being formed by the division of the fusion nuclei in the lower compartments. This situation is certainly very suggestive of a historical relation to the polar fusion in the embryo sac of angiosperms.—J. M. C.

Origin of stipules.—The much debated question of the origin of stipules has received fresh light from the anatomical studies of SINNOTT and

[26] CHRISTY, MILLER, Witches brooms on British willows. Jour. Botany **53**: 97–102. 1915.

[27] EVEREST, ARTHUR E., Recent chemical investigations of the anthocyan pigments and their bearing upon the production of these pigments in plants. Jour. Genetics **45**:361–367. 191.

[28] THOMPSON, W. P., Preliminary note on the morphology of *Gnetum*. Amer. Jour. Bot. **2**:161. 1915.

BAILEY.[29] The former had already concluded that in the primitive angiosperms the vascular supply of the leaves arose as three strands. It is now found that such leaves are usually provided with stipules, the vascular supply of which is connected with the lateral leaf traces; where there is a single leaf trace at the node, stipules are absent, but if the leaf is supplied by many strands it has a sheathing base. It is further observed that leaves with an entire margin generally have no stipules, even though three strands supply the leaf. Stipules are regarded as an integral part of a leaf, and are homologous with sheaths, ligules, and similar modifications of the base of the petiole.—M. A. CHRYSLER.

Scientific phytopathology.—APPEL presented a paper at the twenty-fifth anniversary celebration of the Missouri Botanical Garden which has just been published,[30] dealing with the scientific aspects of plant pathology. This point of view is rapidly developing in this country, but still needs to be emphasized. As APPEL states, until recent times there were no places where scientific phytopathology was taught. The thesis of the paper is illustrated by the biological work in connection with the smut problem, the culture work in establishing polymorphic life histories and, in many identifications, the experimental work on the air content of host tissues, the work in physiological chemistry, and finally the histological study of the host tissues involved.—J. M. C.

A new genus of Erysiphaceae.—ITO[31] has described a new genus (*Typhulocaeta*) of Erysiphaceae from Japan, parasitic on *Quercus glandulifera*. The asci are several in the globose perithecium, and 8-spored; while the appendages are simple and clavate. The conidia have not been observed. The genus is most closely related to *Erysiphe*, but differs in its appendages.—J. M. C.

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[29] SINNOTT, E. W., and BAILEY, I. W., Investigations on the phylogeny of the angiosperms 3. Nodal anatomy and the morphology of stipules. Am. Jour. Bot. 1:441–453. *pl. 44.* 1914.

[30] APPEL, O., The relations between scientific botany and phytopathology. Annals Mo. Bot. Gard. 2:275–285. 1915.

[31] ITO, SEIYA, On *Typhulocaeta*, a new genus of Erysiphaceae. Bot. Mag. Tokyo 29:15–22. *pl. 1.* 1915.